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Estimation of Genetic Parameters for Preweaning Growth Traits of Crossbred Cattle.

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ESTIMATION OF GENETIC PARAMETERS FOR PREWEANING GROWTH TRAITS OF CROSSBRED CATTLE

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DEDICATION

To my mother, the greatest woman in this world

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ABSTRACT

Data from a long-term rotational crossbreeding study involving Angus, Brahman, Charolais and Hereford cattle were analyzed to evaluate the importance of maternal effects on birth weight (BWT), weaning weight (WWT) and preweaning average daily gain (ADG) and, to estimate genetic parameters. Six different animal models were fitted for each trait, ranging from a single additive to a maternal animal model allowing for both genetic and environmental maternal effects and a genetic covariance between direct and maternal additive effects. Genetic effects were obtained using a maternal animal model allowing for a maternal additive effect and a direct-maternal additive covariance (Model 4). All analyses were carried out using MTDFREML. Maternal permanent environmental variance were not important, while maternal additive (MGE) and the direct-maternal (co)variances were important for all traits. Ignoring MGE resulted in overestimates of σ_A^2 and h_A^2. Direct heritability estimates from Model 4 were .35±.05, .55±.07 and .57±.08 for BWT, WWT and ADG, respectively. For the MGE, the corresponding heritabilities were .14±.02, .25±.04 and .30±.04. The direct-maternal genetic correlations were .26±.14, -.36±.09 and -.49±.08 for BWT, WWT and ADG, respectively. Charolais had the greatest positive direct additive genetic influences on preweaning growth traits and had the largest positive maternal additive genetic influence on WWT, compared to the

Hereford breed. The Brahman had positive direct additive genetic influences for BWT and had negative direct additive influences for ADG, compared to the Hereford breed. Angus had negative direct additive genetic effects and had positive maternal additive genetic effects on preweaning growth traits, compared to the Hereford. Brahman was the only breed having a statistically significant maternal additive effect on BWT compared to Hereford. All breeds exhibited positive maternal additive influences on WWT and ADG over Hereford. All direct heterotic effects were positive, except for Angus-Charolais for BWT. Crossbred calves involving the Brahman were the most productive. Birth weight was not influenced by maternal heterosis, except for Charolais-Hereford maternal heterotic effect. Effects involving the Hereford were the only positive and significant maternal heterotic effects on WWT and ADG.

(Key Words: Beef cattle, crossbreeding, preweaning growth traits, maternal effects, genetic parameters, genetic effects).

INTRODUCTION

Crossbreeding is a very useful tool for improving production efficiency of commercial beef cattle (Franke, 1980; Turner, 1980; Cunningham and Magee, 1988). Genetic evaluation of beef cattle invariably depends on the knowledge of genetic parameters appropriate to the conditions where the animals are to be raised. The success of any genetic strategy will depend not only on the precise estimates of these parameters but also on the ability to identify the relevant genetic factors affecting the target trait(s).

Attempts to study and quantify genetic and environmental components of phenotypic (co)variation have been going on since the 1940's. However, considerable progress has been made in the past decade in the ability to partition phenotypic (co)variation into its causal components of (co)variance.

Preweaning growth of a calf can be affected by its own genetic pool as well as by the dam's milk production and mothering ability. Preweaning weight traits, are influenced by the genes received from the sire and dam (direct effects), by the maternal environment provided by the dam (maternal effects) and by interactions among direct and maternal effects.

Knowledge of breed additive and heterotic genetic effects are important in designing effective crossbreeding systems for beef cattle production. Gregory et al. (1980)

pointed out that crossbreeding provides a way to use both nonadditive (heterosis) and additive (breed differences) effects of genes simultaneously. Therefore, an evaluation of breed direct, maternal and non-additive genetic effects is necessary to choose the appropriate breeds and the manner of combining them in a crossbreeding system.

CHAPTER I

REVIEW OF LITERATURE

Introduction

Attempts to study and quantify genetic and environmental components of phenotypic (co)variation have been on going since the 1940's. However, considerable progress has been made in the past decade in the ability to partition phenotypic (co)variation into its causal components of (co)variance. Linear models employed in the genetic evaluation of animals have become more detailed with the increase in computing power. In particular, use of the animal model with restricted maximum likelihood procedures has allowed separation of direct additive genetic effects from maternally additive genetic effects. Biometrical theory and quantitative genetic models were first proposed by Dickerson (1947), Kempthorne (1955) and Willham (1963, 1972). Falconer (1965) and Van Vleck (1971) also contributed to the development of linear genetic models for maternal effects. Preweaning weight traits, as any other maternally influenced trait, seem influenced by the genes received from the sire and dam (direct effects), by the maternal environment provided by the dam (maternal effects) and by interactions among direct and maternal effects. The association between direct and maternal effect is a main question in this context since an antagonistic relationship would have consequences for the breeding program. Therefore, to achieve optimum

progress in selection programs, those factors affecting preweaning growth traits must be identified and quantified.

This literature review will concentrate on more recently published papers that use various models and computing strategies to partition direct and maternal additive genetic effects and maternal environmental components and on the papers discussing genetic theory.

Direct and maternal factors affecting preweaning growth traits

Linear models employed in the genetic evaluation of animals have become more detailed with the increase of computing power. This has resulted in the wide use of the animal model and restricted maximum likelihood (REML) in estimating (co)variance components for maternally influenced traits. An animal model is a linear model which includes a term for the breeding value of the animal making the record (Quaas and Pollak, 1980). Henderson (1988) pointed out that the animal model is actually a set of many different models with the common feature that all animals are evaluated jointly. Quaas and Pollak (1980) were probably the first to use the term "animal model" in their paper about the reduced animal model, but the first application of an animal model is attributed to Henderson (1949). However, it was not until the mid 1980's that the animal model became more popular for the prediction of genetic merit in large populations (Schaeffer and Kennedy, 1986) and for the estimation of

variance components (Graser et al., 1987). In the latter context, the introduction of the DFREML programs by Meyer (1988) provided further momentum.

Under REML, using any likelihood maximization, a likelihood ratio test can be used to test the statistical significance of any subset of the random effects (co)variance parameters. The differences in twice the restricted log likelihood functions (-2log L) between the model with and without the parameter subset is compared to a chi-square distribution with degrees of freedom equal to the difference in dimensions of the parameter subset in question. Many authors have used this technique to study the importance of direct and maternal genetic and maternal permanent environmental components in preweaning growth traits (Tables 1 and 2).

Mrode and Thompson (1990) found a significant effect of both genetic (MGE) and permanent environmental (MCE) maternal effects on weaning weight (WWT) of Simmental cattle. They reported that including either MGE or MCE in the model significantly increased values of log L and decreased estimates of direct additive genetic variance (σ_A^2) by about 40%. Fitting both MGE and MCE as well as the direct-maternal additive genetic covariance did not significantly improve the log L and the maternal additive genetic variance component (σ_M^2) was close to zero. They concluded that the model including direct additive genetic effects (DGE) and MCE

Table 1. Literature estimates for (co)variance components (kg^2) from different models for birth weight

Source/Breed	Model	σ^2_A	σ^2_M	σ^2_C	σ_{AM}	log L[a]
Meyer (1992)	1	10.54	-	-	-	-42.76
	2	9.02	-	1.87	-	-12.48
Hereford	3	7.28	2.63	-	-	-4.18
	4	7.04	2.52	-	.20	-4.14
	5	7.63	1.60	.94	-	-.02
	6	7.46	1.54	.94	.13	.00
Angus	1	7.67	-	-	-	-33.30
	2	6.91	-	1.22	-	-10.59
	3	5.98	1.89	-	-	-3.42
	4	5.10	1.52	-	.76	-2.00
	5	6.18	1.24	.54	-	-1.21
	6	5.36	1.01	.50	.66	.00
Meyer (1993a)	5	7.27	1.21	.52	-	-3.61
Hereford	6	10.21	3.34	.70	-3.33	.00
Meyer (1993b)	1	4.31	-	-	-	-2.22
	2	3.63	-	.86	-	-.14
Charolais	3	3.61	.66	-	-	-.85
	5	3.53	.23	.70	-	.00
Waldron et al (1993)	1	8.40	-	-	-	-
	2	7.20	-	1.90	-	-
Hereford	4	3.80	2.30	-	.90	-
	6	4.00	1.70	.50	1.00	-
Angus	1	6.30	-	-	-	-
	2	5.20	-	1.20	-	-
	4	4.10	1.20	-	.60	-
	6	4.30	.50	.70	.40	-
Angus	1	5.80	-	-	-	-
	2	4.60	-	1.50	-	-
	4	3.50	1.70	-	.20	-
	6	3.80	.80	.90	.20	-

[a]log likelihood expressed as deviation from likelihood value for the most complete model (Model 5 or 6)

Table 2. Literature estimates for (co)variance components (kg^2) from different models for weaning weight

Source	Model	σ^2_A	σ^2_M	σ^2_C	σ_{am}	log L[a]
Meyer (1992)	1	223.00	-	-	-	-236.90
	2	86.50	-	251.50	-	-15.14
Hereford	3	66.20	328.20	-	-	-67.55
	4	130.20	440.50	-	-142.20	-52.81
	5	74.30	58.00	207.80	-	-6.90
	6	120.40	115.50	201.30	-69.20	.00
Angus	1	179.20	-	-	-	-44.64
	2	124.40	-	49.10	-	-14.16
	3	87.90	80.20	-	-	-1.83
	4	77.30	71.70	-	14.70	-1.16
	5	90.70	61.90	13.90	-	-.72
	6	79.10	53.60	14.00	14.50	.00
Zebu cross	1	168.20	-	-	-	-98.24
	2	133.20	-	115.00	-	-37.30
	3	117.30	118.20	-	-	-39.79
	4	301.20	247.80	-	-203.10	-5.40
	5	124.80	55.50	68.20	-	-29.93
	6	294.90	182.20	53.60	-181.40	.00
Meyer (1993a)	5	146.70	77.21	169.86	-	-11.72
Hereford	6	246.75	169.64	169.64	-137.08	0.00
Meyer (1993b)	2	97.60	-	204.50	-	-7.80
	3	109.30	211.00	-	-	-45.37

(table con'd)

Source	Model	σ^2_A	σ^2_M	σ^2_C	σ_{am}	log L[a]
Charolais	5	93.00	26.80	181.00	-	-5.58
	6	177.70	87.60	188.90	-99.90	.00
Mrode and Thompson (1990)	1	397.09	-	-	-	-
	2	241.62	-	98.99	-	-
Simmental	3	238.43	89.07	-	-	-
Waldron et al. (1993)	1	148.60	-	-	-	-
	2	64.10	-	118.10	-	-
Hereford	4	59.10	173.90	-	-40.40	-
	6	60.50	56.40	85.50	-20.70	-
Angus	1	166.30	-	-	-	-
	2	65.90	-	93.50	-	-
	4	45.20	106.80	-	3.00	-
	6	52.70	42.40	56.80	2.80	-
Angus	1	145.20	-	-	-	-
	2	53.10	-	79.90	-	-
	4	46.20	95.30	-	.00	-
	6	47.40	55.70	34.60	.00	-

[a]log likelihood expressed as deviation from likelihood value for Model 6

fitted the data better with similar estimates of σ_A^2, compared to the model including DGE and MGE.

Meyer (1992) fitted six different animal models to study the influences of DGE, MGE and MCE on WWT and birth weight (BWT). Model 1 was a simple additive animal model with the animal additive effects as the only random effect. In Model 2, direct additive genetic effects as well as permanent maternal environmental effects were considered. Model 3 allowed for direct and maternal additive genetic effects but ignored the direct-maternal additive genetic covariance. Model 4 was the same as Model 3 but included the direct-maternal additive genetic covariance. Models 5 and 6 included direct and maternal genetic effects and maternal environmental effects. Model 5 assumed that direct and maternal additive genetic effects were uncorrelated, while Model 6 accounted for the covariance. Meyer (1992) reported that both MGE and MCE significantly influenced variation in BWT; when one ignored maternal effects, inflated estimates of σ_A^2 and h_A^2 were found. However, MGE seemed to be more important than MCE for BWT in both breeds (Hereford and Angus). In the same paper, Meyer reported that WWT variation in Herefords was primarily determined by MCE while in Angus MCE was unimportant when MGE was considered. She concluded that BWT and WWT variability for both breeds considered in her study were best described by a model including both MGE and MCE as well as σ_{AM}, but differences between models with

at least one maternal (MGE or MCE) component were often not significant. The same results were found by Meyer (1993a) using data from a Hereford herd where fitting Model 6 for BWT and WWT dramatically increased the log L. Similar results for WWT were found by Meyer (1993b) in Charolais data with the only exception that σ_{AM} seemed to be not important in explaining variability of WWT. Maternal additive genetic effect explained 4% of phenotypic variance (σ_p^2), while MCE accounted for 23% of σ_p^2. She also found that maternal effects on BWT were mostly non-genetic. MGE explained only 1% of σ_p^2. Therefore, Model 2 was considered the best model for BWT.

In another study, Waldron et al. (1993) used Models 1, 2, 4, and 6 of Meyer (1992) to study BWT and WWT for Angus and Hereford data but they did not report log L. For all breeds and traits considered in this study, σ_A^2 decreased when MCE or MGE was included in the model. This reduction was more than 50% for WWT and at least 14% for BWT. MCE, MGE and σ_{AM} accounted for a large percentage of the variability in WWT. Similar results were observed for BWT of Angus data. In the Hereford herd, MCE appeared unimportant in explaining BWT variability. Therefore, Model 6 seemed most appropriate for WWT in all herds and for BWT in the two Angus herds. Model 4 appeared to give a better fit for BWT in the Hereford data. Swalve (1993) working with Simmental cattle also reported that BWT was better described by Model 4, while Model 6 was the most appropriate for WWT.

Based on published papers, MGE and MCE as well as σ_{AM} seem to greatly affect BWT and WWT. Only one of the reviewed papers reported non-significance of MGE on BWT and WWT. Two of these papers found no effect of MCE on BWT.

Genetic parameters for preweaning growth traits

Parameter estimates for BWT, WWT and average daily gain from birth to weaning (ADG) were reviewed. Tables 3 and 4 present published estimates of direct heritability (h_A^2), maternal heritability (h_M^2), direct-maternal genetic correlation (r_{AM}), proportion of the maternal permanent environmental variance (σ_C^2) to the σ_P^2 (p_c) and total heritability (h_T^2) for different breeds of beef cattle. In the early 80's, Burfening et al. (1981), using a sire-maternal grandsire model (S-MGS) for Simmental BWT records, found that h_M^2 was smaller than h_A^2. The corresponding heritabilities were .21 for h_A^2 and .11 for h_M^2. The genetic correlation between DGE and MGE was -.24. Similar results for BWT were found by Quaas et al. (1985) with Simmental cattle. The h_A^2 was .16 while h_M^2 was .06. However, in this study r_{AM} was positive (.44). For WWT, these authors published values of .12, .08 and -.04 for h_A^2, h_M^2 and r_{AM}, respectively. Bertrand and Benyshek (1987) reported that direct additive and maternal genetic variances were very similar for WWT in Limousin (.16 and .15) while h_A^2 was larger than h_M^2 in Brangus (.28 and .20).

Table 3. Literature estimates for genetic parameters for birth weight

Source	h_A^2	h_M^2	r_{AM}	p_e	h_T^2	Breed[a]
Burfening et al. (1981)	.21	.11	-.24	-	-	S
Quaas et al. (1985)	.16	.06	.44	-	-	S
Bertrand and	.22	.05	-.16	-	-	L
Benyshek (1987)	.25	.13	-.12	-	-	R
Trus and Wilton (1988)	.37	.13	-.34	-	.32	A
	.39	.13	-.39	-	.32	H
	.27	.20	.55	-	.56	O
	.42	.17	-.39	-	.35	C
	.34	.20	-.22	-	.36	S
Garrick et al. (1989)	.44	.12	-.38	-	-	S
Brown et al. (1990)	.42	.22	-.12	-	-	A
	.58	.22	-.13	-	-	H
Kriese et al. (1991)	.37	.18	-.15	-	-	B
	.28	.12	-.52	-	-	R
Mackinnon et al. (1991)	.61	.11	.01	-	-	Z
Meyer (1992)	.41	.08	.04	.05	.46	H
	.36	.07	.28	.03	.46	A
Meyer (1993a)	.61	.17	-.64	.05	.39	H
Meyer (1993b)	.21	-	-	.05	-	C
Shi et al. (1993)	.31	.08	-.40	.05	.26	L
Swalve (1993)	.42	.08	-	-	-	S
Waldron et al. (1993)	.23	.14	.30	-	.39	H
	.33	.04	.28	.06	.40	A
	.32	.06	.13	.07	.37	A
Arthur et al. (1994a)	.53	.18	-.35	-	.46	H
Lobo et al. (1994)	.29	-	-	-	-	N
Pang et al. (1994)	.65	.19	-.11	-	.69	H

[a]A=Angus; B=Brahman; R=Brangus; C=Charolais; Hereford; L=Limousin; N=Nellore; S=Simmental; O=Shorthorn; Z=Zebu crosses

Table 4. Literature estimates for genetic parameters for weaning weight

Source	h^2_A	h^2_M	r_{AM}	p_c	h^2_T	Breed[a]
Quaas et al. (1985)	.12	.08	-.04	-	-	S
Bertrand and	.16	.15	-.30	-	-	L
Benyshek (1987)	.28	.20	-.29	-	-	R
Garrick et al. (1989)	.36	.19	-.32	-	-	S
Brown et al. (1990)	.63	.16	-.36	-	-	A
	.66	.43	-.08	-	-	H
Kriese et al. (1991)	.23	.16	.15	-	-	B
	.21	.15	-.23	-	-	R
Mackinnon et al. (1991)	.20	.32	.00	-	-	Z
Meyer (1992)	.14	.13	-.59	.23	.08	H
	.20	.14	.22	.04	.32	A
	.58	.36	-.78	.11	.23	Z
Meyer (1993a)	.20	.18	-.45	.16	.16	H
Meyer (1993b)	.12	.04	-	.23	-	C
Mrode and Thompson (1993)	.19	-	-	.08	-	S
Shi et al. (1993)	.26	.13	-.25	.09	.25	L
Swalve (1993)	.44	.08	-	.16	-	S
Waldron et al. (1993)	.15	.14	-.35	.21	.14	H
	.14	.11	.06	.15	.21	A
	.13	.15	.00	.09	.20	A
Arthur et al. (1994a)	.06	.41	-.98	-	.03	H
Lobo et al. (1994)	.25	-	-	-	-	N
Pang et al. (1994)	.07	.76	-.99	-	.10	H

[a]See Table 3 for abbreviations and footnotes

In both breeds the r_{AM} for WWT were similar, -.30 in Limousin and -.29 in Brangus. For BWT, these researchers reported .22, .05 and -.16 for h^2_A, h^2_M, and r_{AM} in Limousin. The corresponding values for Brangus were .25, .13 and -.12, respectively.

Trus and Wilton (1988) showed a negative genetic correlation between direct additive and maternal genetic effects for BWT of several breeds, with the exception of Shorthorn. These r_{AM} ranged from -.22 to -.39. For Shorthorn it was .55. The h^2_A were larger than h^2_M for all breeds. They were .37 and .13 for Angus, .39 and .13 for Hereford, .27 and .20 for Shorthorn, .42 and .17 for Charolais, and .34 and .20 for Simmental. In the same study, r_{AM} for ADG were negative for all breeds. These values ranged from -.14 in Shorthorn to -.54 in Angus. The h^2_A for this trait were .39, .30, .39, .27 and .43 for Angus, Hereford, Shorthorn, Charolais and Simmental, respectively. The corresponding h^2_M were .21, .27, .26, .16, and .20. Garrick et al. (1989) found a direct heritability of .44 for BWT and .36 for WWT. The h^2_M for BWT was .12, while for WWT it was .19. The r_{AM} was negative for both traits (-.38 for BWT and -.32 for WWT). In another similar study, Brown et al. (1990) reported h^2_A of .42 and .58 for BWT of Angus and Hereford. The h^2_M was the same for both breeds (.22). The r_{AM} was -.12 for Angus and it was -.13 for Hereford. For WWT, they reported .63, .16 and -.36 for h^2_A,

h^2_M and r_{AM} in Angus. The corresponding values for Hereford were .66, .43 and -.08.

With the increase in computing power over the last four years, many papers have been published on use of the animal model to estimate genetic parameters. Kriese et al. (1991) applied a maternal animal model (an animal model including terms for maternal effects) to preweaning growth traits of Brahman and Brangus. The direct heritability for BWT was .37 in Brahman and .28 in Brangus, while they were .23 and .21 for WWT. The maternal heritability for Brahman was .18 for BWT and .16 for WWT, while they were .12 and .15 for Brangus. The r_{AM} were negative except for WWT of Brahman.

Mackinnon et al. (1991) used a maternal animal model to analyze BWT and WWT of Zebu crosses. They found a h^2_A of .61 for BWT and .20 for WWT. The maternal heritability was .11 for BWT and .32 for WWT. The r_{AM} was almost zero for both traits. Mrode and Thompson (1990), using the same technique on WWT of Simmental cattle, published values of .19 for h^2_A and .08 for p_c. A similar value for h^2_A was published by Meyer (1992) for WWT of Angus and Hereford. However, the estimate of the same parameter in Zebu cross was much larger (.58). The h^2_M were .13, .14 and .36 for Hereford, Angus and Zebu cross, respectively. The p_c was larger in Hereford than in Angus and Zebu crosses (.23 vs .04 and .11). A negative r_{AM} was found for Hereford and Zebu crosses (-.59 and -.78), while for Angus it was positive (.22). Meyer also found that

h^2_A, h^2_M and p_c for BWT were very close for both pure breeds (.41 and .36 for h^2_A, .08 and .07 for h^2_M and .05 and .03 for p_c). But, r_{AM} was larger for Angus (.28) than for Hereford (.04).

Meyer (1993a) using a maternal animal model detected that 61% of BWT variability in Hereford was explained by the direct additive genetic variance, 17% by the maternal genetic variance and 5% by the permanent environmental variance due to the dam. The r_{AM} was -.64. For WWT, she reported values of .20 for h^2_A, .18 for h^2_M and .16 for p_c. The r_{AM} was also large and negative (-.45). In another study with Charolais cattle, Meyer (1993b) found a h^2_A of .21 and .05 for p_c. The corresponding values for WWT were .12 and .23. The MGE explained only 4% of the variability of WWT. Waldron et al. (1993) reported similar values of h^2_A and h^2_M for WWT of two Angus herds and one Hereford herd; but the p_c and r_{AM} varied with the herd. For Hereford, the p_c and r_{AM} were .21 and -.35, while for one of the Angus herds they were .15 and .06. In the other Angus herd, the p_c was .09 while the r_{AM} was zero. In this study and for BWT, these authors reported .23, .33 and .32 as the magnitude of h^2_A for Hereford and the two Angus herds. The h^2_M was .14 in Hereford and close to zero in the Angus herds. The p_c were also close to zero. The direct-maternal genetic correlation was .30 in Hereford and .28 and .13 in Angus.

Shi et al. (1993) evaluated BWT and WWT of Limousin cattle using Model 6 of Meyer (1992). They established that 31%, 8% and 5% of the variability of BWT were attributed to DGE, MGE and MCE, respectively. For WWT, they were .26 for h_A^2, .13 for h_M^2 and .09 for p_c. The r_{AM} was negative for BWT (-.40) and positive for WWT (.09).

Nellore records from Brazil were analyzed by Lobo et al. (1994) using an additive animal model. They reported h_A^2 of .29 for BWT and .25 for WWT. Arthur et al. (1994a), using a maternal animal model on Hereford data, found direct and maternal heritabilities of .53 and .18 for BWT. For WWT, they were .06 and .41. The r_{AM} was negative for both traits (-.35 for BWT and -.98 for WWT). Pang et al. (1994) also analyzed Hereford preweaning data. They found that direct heritability for WWT and ADG were lower than maternal heritibility, but for BWT it was higher. The genetic correlation between direct and maternal effects were negative for all traits.

In summary, direct heritability seems to be more important than maternal heritability for both traits, BWT and WWT. The h_A^2 for BWT averaged .37, while h_M^2 was .13. For WWT, the maternal heritability accounted for 21% and direct heritability explained at least 25% of the total WWT variability. There was a wide range in estimates for p_c, but it was much less important than maternal additive heritibility. The direct-maternal additive genetic

correlation was negative for WWT. Fourteen out of 19 estimates were negative, averaging -.42. For BWT, 16 estimates were negative (r_{AM}=-.28 on average) and eight were positive (r_{AM}=.25 on average).

Breed-direct and breed-maternal additive genetic effects for preweaning growth traits

Crossbreeding is an effective tool to improve traits of economic importance in beef cattle. However, an evaluation of breeds of cattle for crossbreeding systems requires the study of their direct, maternal, and non-additive genetic effects (Willham, 1970). Dickerson (1969, 1973) described the theory of crossbreeding schemes and provided definitions for different genetic effects that might be considered in the evaluation of breeds for mating systems. Effective crossbreeding systems are based on exploitation of breed and heterosis effects. Efficient use of breed effects is based on knowledge of both direct and maternal breed characteristics. Tables 5, 6 and 7 present published estimates for direct and maternal additive genetic effects for preweaning growth traits.

Olson et al. (1993) evaluated genetic effects of BWT and WWT for Angus, Brahman and Charolais breeds and breed combinations. They reported values for direct additive effects of Brahman as a deviation from Angus of 6.1 kg for BWT and 8.0 kg for WWT. The direct additive effect of Charolais on BWT and WWT was large, 13.0 kg for BWT and 52.2

Table 5. Direct (g^I) and maternal (g^M) additive genetic effects for BWT

Source Breed	Breed[a]	g^I(kg)	g^M(kg)
Koch et al. (1985)[b]	A	-1.3*	- .1
Roberson et al. (1986)[b]	B	4.6± .6*	-7.5± .5*
Wyatt and Franke (1986)[c]	B	7.4± .2*	-6.1± .2*
	R	3.3± .5*	-.5± .4
	W	5.5± .5*	4.6± .4*
	C	12.7± .7*	-2.6± .7*
	H	2.6± .2*	.1± .1
	G	6.7± .5*	-1.2± .4*
	S	6.6±1.7*	3.1±1.0*
	O	5.7± .4*	-1.6± .4
Comerford et al. (1987)[d]	S	0.2	1.4
	L	-1.0	3.0*
	H	-1.8	2.3*
	B	2.5	-6.7*
Cunningham and Magee (1988)[b]	A[e]	-3.4±1.7*	2.9±1.9
	C[e]	-1.3±1.9*	6.4±1.9*
	A[f]	-9.5±2.6*	8.0±2.1*
	C[f]	-2.3±2.7	4.4±2.5
	S[f]	-.04±2.2	4.3±2.4*
Olson et al. (1993)[c]	B	6.1±0.9*	-4.2±0.7*
	C	13.0±1.0*	-.7±0.8
Arthur et al. (1994b)[b]	B[g]	3.8±2.7	-8.2±3.0*
	B[h]	1.7±2.2	-5.3±2.5*
	B[i]	3.7±2.6	-3.2±2.9

[a]A=Angus; B=Brahman; R=Brangus; W=Brown Swiss; C=Charolais; H=Hereford; L=Limousin; G=Santa Gertrudis; O=Shorthorn; S=Simmental; Z=Zebu crosses
[b]Regression coefficients deviated from Hereford
[c]Regression coefficients deviated from Angus
[d]General combining ability
[e]dataset 1
[f]dataset 2
[g]Values on high quality pasture
[h]Values on medium quality pasture
[i]Values on low quality pasture
*$p<.05$

Table 6. Direct (g^I) and maternal (g^M) additive genetic effects for WWT

Source Breed	Breed[a]	g^I(kg)	g^M(kg)
Koch et al. (1985)[b]	A	-5.4*	11.0*
Roberson et al. (1986)	B	-12.9± 2.7*	13.1± 2.5*
Wyatt and Franke (1986)[c]	B	2.5± 1.4	3.7± 1.4*
	R	8.6± 2.8*	16.5± 2.5*
	W	25.8± 2.9*	29.8± 2.3*
	C	42.0± 3.8*	4.1± 3.9
	H	3.2± 0.8*	-9.5± .8*
	G	15.8± 2.9*	20.7± 2.6*
	S	57.9± 9.8*	-12.2± 5.8*
	O	13.4± 2.2*	-17.5± 2.4*
Comerford et al. (1988)[d]	S	4.0	4.8
	L	-6.8	.7
	H	-5.9	-13.4*
	B	8.7	7.9
Cunningham and Magee (1988)[b]	A[e]	-29.7±10.7*	23.6±10.8*
	C[e]	-13.6±11.3*	13.5±11.2
	A[f]	-8.5±12.8	46.3±10.1*
	C[f]	10.6±12.5	7.4±12.0
	S[f]	18.8±11.0	30.6±12.0*
Olson et al. (1993)[c]	B	8.0± 4.0*	2.2± 3.1
	C	52.2± 3.9*	2.7± 3.3
Arthur et al. (1994b)[b]	B[g]	-23.3±15.5	-28.5±17.6
	B[h]	-14.4±13.1	-8.5±14.9
	B[i]	-18.6±14.9	64.8±16.6*

See Table 5 for abbreviations and footnotes

Table 7. Direct (g^I) and maternal (g^M) additive genetic effects for ADG

Source Breed	Breed[a]	g^I(kg/d)	g^M(kg/d)
Koch et al. (1985)[b]	A	-.020*	.054*
Roberson et al. (1986)[b]	B	-.098±.014*	.111±.013*
Wyatt and Franke (1986)[b]	B	-.022±.006*	.045±.006*
	R	.028±.012*	.078±.011*
	W	.104±.012*	.123±.010*
	C	.124±.017*	.031±.017
	H	-.000±.004	-.041±.003*
	G	.039±.012*	.097±.011*
	S	.233±.042*	-.064±.025*
	O	.040±.009*	-.073±.010*
Comerford et al. (1988)[d]	S	.020	.010
	L	-.020	-.010
	H	-.020	-.070*
	B	.020	.070
Cunningham and	A[e]	.100±.004*	.110±.040*
Magee (1988)[b]	C[e]	-.030±.040	.040±.040
	A[f]	-.002±.062	.190±.049*
	C[f]	.010±.060	.026±.058
	S[f]	.002±.054	.110±.058
Arthur et al. (1994b)[b]	B[g]	-.045±.050	-.012±.055
	B[h]	.002±.041	.007±.047
	B[i]	-.037±.052	.270±.059*

See Table 5 for abbreviations and footnotes

kg for WWT. The maternal additive effect of Brahman found in this study was -4.2 kg for BWT, as a deviation from Angus. The Angus and Charolais maternal additive effects on BWT were similar. The three breeds also showed similar maternal additive effects on WWT.

Arthur et al. (1994b) analyzed genetic effects of BWT, WWT and ADG for Hereford and Brahman breeds and first-crosses and back-crosses of these breeds. The Brahman maternal additive effects on BWT were negative on high and medium quality pastures, compared to Hereford. On low quality pasture, there was a positive significant Brahman maternal additive effect on WWT (64.8 kg) and ADG (.270 kg/d). The other additive effects were not significant.

Wyatt and Franke (1986) analyzed preweaning data for straightbred and crossbred beef cattle from 25 locations across 10 Southern states. Direct additive genetic effects for BWT and WWT were positive and significantly different from Angus for all breeds except WWT of Brahman. Brahman, Brown Swiss, Santa Gertrudis, Simmental, and Shorthorn had similar direct additive effects for BWT. Charolais had the largest direct additive effect for BWT, while Brangus and Hereford had the smallest values. The Simmental direct additive effect for WWT was the largest followed by the Charolais and Brown Swiss direct additive effects. The Hereford direct additive effect for WWT was small but still statistically different from the Angus direct effect.

Shorthorn, Santa Gertrudis and Brangus showed similar direct additive effects for WWT. Simmental, Charolais and Brown Swiss had the largest direct additive effect for ADG with Brahman being negative and Hereford similar to Angus. The other breeds had positive direct additive effects for ADG. All maternal additive effects were significant, except those of Charolais for both WWT and ADG and Brangus, Hereford and Shorthorn for BWT. The largest maternal additive effects for all three traits were attributed to Brown Swiss. Brahman and Santa Gertrudis maternal additive effects were negative for BWT and positive for WWT and ADG. Simmental, Hereford and Shorthorn maternal additive effects were negative for both WWT and ADG.

Comerford et al. (1987) compared the genetic effects of Simmental, Limousin, Polled Hereford and Brahman breeds in a diallel mating pattern for BWT. None of the general combining abilities (GCA) among the four breeds were statistically different from zero. The maternal specific combining ability (SCA) effects were only non-significant for Simmental. Limousin and Hereford SCA effects were similar and positive, while Brahman showed a negative SCA effect. Using data from the same herd, Comerford et al. (1988) found that GCA effects on WWT and ADG were not important. Significant negative SCA effects were found for Hereford for both WWT and ADG. The other maternal effects were not significantly different from zero.

Roberson et al. (1986) evaluated preweaning growth data on Brahman, Hereford and Brahman-Hereford crosses. The estimate of Brahman direct additive effects on BWT, WWT, and ADG compared with the Hereford effect were 4.6 kg, -12.9 kg and -.098 kg/d, respectively. The Brahman maternal additive effects were 7.5 kg less than Hereford for BWT, 13.1 kg larger for WWT and .111 kg/d larger for ADG.

Koch et al. (1985) used purebred, F_1, backcrosses, and F_2 and F_3 inter se combinations of Angus and Hereford to estimate genetic effects. Direct additive effects indicated that Angus, compared with Hereford, had calves that had lower BWT, WWT and ADG. Differences in breed maternal additive effects were not significant for BWT, but significantly positive for WWT and ADG.

Cunningham and Magee (1988) found that the Angus and Charolais direct additive effects on BWT were negative compared to the Hereford breed with the Angus being most negative. For WWT, it was significantly negative for Angus and Charolais in dataset 1 (record from 1972-1976) but not significant for any breed in dataset 2 (records from 1978-1982). Direct and maternal breed effects on ADG for Charolais and Simmental were very small and insignificant except for Angus. Angus and Simmental maternal effects were positive for both BWT and WWT. The maternal effects of Charolais on BWT and WWT were positive but only significant for BWT in dataset 1.

Individual and maternal heterosis for preweaning growth traits

Estimates of direct and maternal heterotic effects from the literature are presented in Tables 8, 9 and 10. Olson et al. (1993) found significant positive direct heterosis estimates of 3.4 kg for BWT and 35.9 kg for WWT in Angus x Brahman crosses. This heterosis effect was not important for Angus-Charolais. The direct heterosis effect of Brahman-Charolais was not significant for BWT but was for WWT (19.9 kg). Maternal heterotic effects due to Angus-Brahman heterozygosity resulted in increased BWT (2.9 kg) and WWT (21.4 kg). Angus-Charolais and Brahman-Charolais maternal heterosis was not significant for BWT, but it was positive and significant for WWT (7.4 kg for Angus-Charolais and 22.1 kg for Brahman-Charolais).

Arthur et al. (1994b) reported a significant direct heterosis for BWT among Brahman-Hereford crosses on medium quality pasture and for WWT and ADG on high and medium quality pasture. Maternal heterotic effects were significant and positive for WWT on all three quality pastures. They were also significant for ADG on medium and low quality pastures, but not on high quality pastures.

Wyatt and Franke (1986) found that direct heterosis estimates on preweaning growth traits, in general, were positive. Angus-Shorthorn and Charolais-Santa Gertrudis direct heterosis estimates were negative for BWT, WWT and

Table 8. Direct (h^I) and maternal (h^M) heterotic effects for BWT

Source Breed	Breed[a]	h^I(kg)	h^M(kg)
Koch et al. (1985)	A-H	0.8*	1.0*
Roberson et al. (1986)	B-H	2.2±0.3*	.6±0.3*
Wyatt and Franke (1986)	A-B	2.9±0.2*	1.0±0.2*
	A-R	1.1±0.4*	1.0±0.5*
	A-W	0.1±0.3	-0.3±0.2
	A-C	-1.7±0.4*	1.0±0.4*
	A-H	0.2±0.1*	-0.9±0.1*
	A-G	1.6±0.3*	-
	A-S	1.6±0.9	-3.3±0.6*
	A-O	-0.9±0.3*	0.4±0.4
	B-R	0.4±0.4	-
	B-W	3.4±0.6*	-
	B-C	-0.3±0.5	-
	B-H	2.9±0.2*	0.8±0.2*
	R-H	1.7±0.4*	-
	W-H	1.0±0.4*	-1.4±0.5*
	C-H	-1.7±0.4*	1.8±0.4*
	C-G	-0.2±1.1	-
	C-S	1.4±1.2	-
	H-G	0.9±0.3*	-
	H-S	1.9±0.9*	-1.3±0.5*
	H-O	1.8±0.5*	1.7±0.3*
	G-O	3.5±1.5*	-
Comerford et al. (1987)[j]	S-L	-0.3	
	S-H	-1.0	
	S-B	0.8	
	L-H	-0.7	
	L-B	1.3	
	H-B	2.6*	
Olson et al. (1993)	A-B	3.4±0.8*	2.9±0.7*
	A-C	1.2±0.8	1.0±0.7
	B-C	-0.2±0.8	1.0±0.7
Arthur et al. (1994b)	B-H[g]	3.3±2.1	-1.2±1.2
	B-H[h]	6.5±1.7*	-1.1±1.0
	B-H[i]	1.5±2.0	1.6±1.2

[a]See Table 5 for abbreviations and footnotes
[j]Heterotic effects included both h^I and h^M

Table 9. Direct (h^I) and maternal (h^M) heterotic effects for WWT

Source Breed	Breed[a]	h^I(kg)	h^M(kg)
Koch et al. (1985)	A-H	6.9*	12.8*
Roberson et al. (1986)	B-H	21.6± 1.5*	19.8±1.4*
Wyatt and Franke (1986)	A-B	24.2± 1.0*	13.0±1.1*
	A-R	3.9± 2.2*	1.1±2.6
	A-W	3.0± 1.8	7.8±1.3*
	A-C	-0.9± 2.1*	1.4±2.2
	A-H	4.8± 0.6*	4.0±0.7*
	A-G	15.3± 1.8*	-
	A-S	-8.4± 5.1	-0.5±3.2
	A-O	-2.2± 1.9	5.7±2.3*
	B-R	10.8± 2.4*	-
	B-W	11.3± 3.6*	-
	B-C	18.9± 3.0*	-
	B-H	23.7± 1.0*	17.7±0.8*
	R-H	14.0± 2.5*	-
	W-H	2.3± 2.0	-2.4±3.1
	C-H	0.8± 2.1	7.5±2.1*
	C-G	-16.7± 6.3*	-
	C-S	-27.9± 6.6*	-
	H-G	12.9± 1.8*	-
	H-S	-8.7± 5.2	14.2±2.9*
	H-O	14.3± 3.0*	13.8±1.7*
	G-O	43.1± 8.6*	-
Comerford et al. (1988)[j]	S-L	1.1	
	S-H	11.4*	
	S-B	20.4*	
	L-H	8.6*	
	L-B	16.9*	
	H-B	20.3*	
Olson et al. (1993)	A-B	35.9± 3.2*	21.4±2.7*
	A-C	3.8± 3.3	7.4±2.9*
	B-C	19.9± 3.4*	22.1±2.9*
Arthur et al. (1994b)	B-H[g]	24.9±12.4*	14.9±7.1*
	B-H[h]	20.2±10.1*	30.9±5.8*
	B-H[i]	19.7±11.6	37.8±6.9*

See Tables 5 and 8 for abbreviations and footnotes

Table 10. Direct (h^I) and maternal (h^M) heterotic effects for ADG

Source Breed	Breed[a]	h^I(kg)	h^M(kg/d)
Koch et al. (1985)	A-H	.031*	.057*
Roberson et al. (1986)	B-H	.109±.008*	.108±.007*
Wyatt and Franke (1986)	A-B	.100±.004*	.052±.004*
	A-R	.010±.009	-.001±.011
	A-W	.012±.008	.034±.006*
	A-C	.005±.009	.023±.010*
	A-H	.020±.002*	.022±.003*
	A-G	.055±.008*	-
	A-S	-.050±.022*	.019±.014
	A-O	-.004±.008	.021±.010*
	B-R	.047±.010*	-
	B-W	.062±.015*	-
	B-C	.098±.013*	-
	B-H	.099±.004*	.081±.004*
	R-H	.051±.011*	-
	W-H	.001±.009	-.009±.013
	C-H	.010±.009	.028±.009*
	C-G	-.077±.027*	-
	C-S	-.151±.030*	-
	H-G	.054±.008*	-
	H-S	-.050±.022*	.075±.012*
	H-O	.058±.013*	.057±.007*
	G-O	.158±.037*	-
Comerford et al. (1988)[j]	S-L	.010	
	S-H	.050*	
	S-B	.090*	
	L-H	.040*	
	L-B	.080*	
	H-B	.090*	
Arthur et al. (1994b)	B-H[g]	.079±.040*	.031±.022
	B-H[h]	.068±.032*	.105±.018*
	B-H[i]	.061±.041	.153±.025*

See Tables 5 and 8 for abbreviations and footnotes

ADG. Angus-Charolais, Angus-Simmental, Charolais-Simmental, and Hereford-Simmental direct heterosis estimates were positive for BWT but negative for both WWT and ADG, while Brahman-Charolais and Charolais-Hereford estimates were negative for BWT and positive for WWT and ADG. These authors published significant maternal heterosis estimates for Angus-Brahman, Angus-Hereford, Brahman-Hereford, Charolais-Hereford, Hereford-Simmental, and Santa Gertrudis-Shorthorn crosses on all preweaning growth traits. Maternal heterotic effects for Angus with Brown Swiss and Shorthorn were not significant for BWT but significant for the other two traits. On the contrary, this maternal heterosis effect was significant for Angus-Brangus, Angus-Simmental, and Brown Swiss-Hereford for BWT but not for WWT and ADG. Angus-Charolais maternal heterosis was important for BWT and ADG.

In the study by Comerford et al. (1987), heterotic effects on BWT were only important for the Hereford-Brahman breed combination. The heterotic effects on WWT and ADG were positive and significant, except for Simmental-Limousin.

Roberson et al. (1986) found that the Brahman-Hereford direct heterotic effect on BWT was 2.2 kg, while maternal heterosis was .6 kg. Direct and maternal heterotic effects on WWT were 21.6 kg and 19.8 kg, respectively. For ADG, they were .109 kg/d and .108 kg/d. Positive and significant heterosis was found by Koch et al. (1985) for Angus-Hereford crosses. Direct heterosis estimates of BWT, WWT and ADG were

.8 kg, 6.9 kg and .031 kg/d, respectively. The corresponding maternal heterosis estimates were 1.0 kg, 12.8 kg and .057 kg/d.

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CHAPTER II

VARIANCE COMPONENT ESTIMATION FOR PREWEANING GROWTH TRAITS OF CROSSBRED CATTLE

Introduction

Genetic evaluation of beef cattle invariably depends on the knowledge of genetic parameters appropriate to the conditions where the animals are to be raised. The success of any genetic strategy will depend not only on the precise estimates of these parameters but also on the ability to identify the relevant genetic factors affecting the target trait(s). Preweaning growth traits of a calf can be affected by its own genetic makeup as well as by the dam's milk production and mothering ability. Therefore, the objectives of this study were to:

1. Evaluate the importance of direct and maternal additive genetic, and maternal environmental (co)variances for preweaning growth traits of crossbred calves involving Angus, Brahman, Charolais and Hereford breeding.
2. Estimate heritability and genetic correlations among preweaning growth traits of crossbred cattle.

Materials and Methods

Source of data Pre-weaning growth trait records for this study came from four generations of a long-term rotational crossbreeding study conducted at the Ben Hur Beef Cattle Crossbreeding Unit of the Louisiana Agricultural Experiment Station, Baton Rouge, Louisiana. Baton Rouge is located at

latitude 30°31′ N and longitude 91°08′ W and is 10.8 m above sea level. The climate is subtropical with average daily minimum and maximum temperature of 18 and 26 °C, average daily minimum and maximum humidity of 45 and 88%, and average annual rainfall of 147 cm (LAIS, 1989).

This crossbreeding experiment included four straightbred and seven rotational crossbred lines. The four straightbred lines used as controls were Angus (A), Brahman (B), Charolais (C) and Hereford (H). The crossbred lines were the three two-breed (A-B, C-B and H-B), three three-breed (A-B-C, A-B-H, and B-C-H), and one four-breed (A-B-C-H) rotational mating system combinations that included B. These crossbred lines were initiated with F_1 A-B, C-B and H-B cows in generation one. The total number of records per line in each generation is presented in Table 11. Each generation lasted for four years with no overlapping.

Variables used in this study included generation, calf year of birth, calf julian birthdate, cow line, calf weaning age, sex of calf, cow age at parturition, and sire, cow and calf identification. A total of 16 years was evenly distributed through the four generations. Age of cow at parturition ranged from two to 18 years. Pre-weaning growth traits of interest were birth weight (BWT), weaning weight (WWT) and average daily gain (ADG). Birth weight and weaning eights were adjusted to a male and mature cow basis before analysis. In addition, weaning weight was adjusted to 205 d

Table 11. Number of records per cow line in each generation

Line	Generation 1	2	3	4
Straightbreds				
Angus (A)	104	78	89	77
Brahman (B)	72	75	63	63
Charolais (C)	92	72	90	68
Hereford (H)	77	72	104	79
Two-breed rotation				
A-B	82	78	89	78
C-B	92	81	100	78
H-B	97	90	118	76
Three-breed rotation				
A-B-C	83	96	107	87
A-B-H	116	104	104	103
B-C-H	84	99	96	85
Four-breed rotation				
A-B-C-H	87	76	102	92
Total	986	921	1062	886

weaning age. The adjustment factors were those recommended by BIF (1990). Individual average daily gain from birth to weaning was calculated using the adjusted birth and weaning weights. Data and pedigree information used in this analysis spanned years of birth from 1970 to 1988.

Management of cattle All cattle were maintained on common bermuda (*Cynodon dactylon*) and dallisgrass (*Paspalum dilatatum*) pastures during the summer with Louisiana S1 white clover (*Trifolium repens*) available in the spring. In the winter, cows were fed on native hay, 32% protein fortified blackstrap molasses and grazed overseeded ryegrass (*Lolium multiflorum*). Before each breeding season, 25 to 30 cows were randomly assigned to single-sire breeding herds based on their age and breed-type. Only purebred sires were used. These sires came from Louisiana breeders and from other Louisiana Agricultural Experiment Station research centers. Bulls were purchased at one or two years of age based on their yearling weight and size, structural soundness, and fertility of their dams. Sires were used for only two breeding seasons in order to sample as many bulls as possible within each breed. Prior to the start of each breeding season, bulls were weighed, dewormed, and required to pass a breeding soundness examination. The breeding season lasted for 75 days, beginning April 15 and ending July 1 of each year.

The calving season started about January 15 and ended shortly after April 1 each year. At birth, calves were weighed, dehorned and identified by ear notch. All bull calves were castrated in the first week of July and all calves were vaccinated for calfhood diseases. Calves were weaned the first week of October at an average age of 220 days. Cows were pregnancy tested in October and were culled only for failing to produce a calf for two consecutive years, structural unsoundness or reproductive abnormalities. No deliberate selection was placed on heifers for growth performance, or on mature females for production.

Statistical analysis Pre-weaning growth traits were analyzed using an animal model and the MTDFREML program (Boldman et al., 1993). Under this set of programs, variance and covariance components are estimated by Restricted Maximum Likelihood (Patterson and Thompson, 1971) using a derivative-free algorithm (Graser et al., 1987). Direct and maternal genetic effects and the maternal environmental effect were taken into account by including animal (calf) as a correlated random effect and dam of calf as correlated and uncorrelated random effects (Meyer, 1989).

Preliminary analyses suggested a significant effect of cow line, generation and their interaction. Consequently, Line-Generation combination was included as a main fixed effect in all models. Year of calf birth and julian birthdate variation were accounted for by fitting these as

linear and quadratic covariables as indicated by preliminary analyses.

Univariate and multiple-trait analyses were conducted. Six different univariate-trait models were analyzed (Meyer, 1992a). Model 1 was a simple additive animal model with the animal's additive effect as the only random effect. In Model 2, the direct additive genetic effect as well as maternal environmental effects were considered. Dam was included as an uncorrelated random effect. Model 3 allowed for direct and maternal additive genetic effects but ignored any covariance. Dam was fitted as an additional correlated random effect with the same covariance structure as the direct additive genetic effects. Model 4 was the same as Model 3 but allowed for a direct-maternal covariance. Models 5 and 6 included direct and maternal genetic and maternal environmental effects. Model 5 assumed that direct and maternal effects were uncorrelated, while Model 6 accounted for it. The six models were:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{e} \qquad (1)$$

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_2 + \mathbf{e} \qquad (2)$$

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{u}_1 + \mathbf{Z}_2\mathbf{u}_3 + \mathbf{e}$$
$$\text{with } \mathrm{Cov}(\mathbf{a},\mathbf{m}) = \mathbf{0} \qquad (3)$$

$$y = X\beta + Z_1u_1 + Z_2u_3 + e \quad \text{with } Cov(a,m) \neq 0 \tag{4}$$

$$y = X\beta + Z_1u_1 + Z_2u_2 + Z_2u_3 + e \quad \text{with } Cov(a,m) = 0 \tag{5}$$

$$y = X\beta + Z_1u_1 + Z_2u_2 + Z_2u_3 + e \quad \text{with } Cov(a,m) \neq 0 \tag{6}$$

where

y = vector of observations;

β = vector of unknown fixed effects, including line-generation and linear and quadratic covariables of year of calf birth and julian birthdate;

X = known design matrix relating records to the fixed effects in the model;

u_1, u_2, u_3 = vectors of unknown random effects for calf and calf's dam;

Z_1, Z_2 = known design matrices relating records to the random effects in the model;

e = vector of random residual effects.

The variance-covariance structure for the random effects in this analysis was assumed to be:

$$V\begin{bmatrix} u_1 \\ u_2 \\ u_3 \\ e \end{bmatrix} = \begin{bmatrix} \sigma_A^2A & 0 & \sigma_{AM}A & 0 \\ 0 & \sigma_C^2I & 0 & 0 \\ \sigma_{AM}A & 0 & \sigma_M^2A & 0 \\ 0 & 0 & 0 & \sigma_c^2I \end{bmatrix}$$

where σ_A^2 refers to the direct additive genetic variance, σ_M^2 the maternal additive genetic variance, σ_{AM} the additive genetic covariance between direct and maternal effects, σ_C^2 the permanent environmental maternal variance, σ_e^2 the residual variance, **A** the numerator relationship matrix, and **I** is an identity matrix.

For the most complete model, Model 6, the mixed model equations can be written as follows:

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z_1} & \mathbf{X'Z_2} & \mathbf{X'Z_2} \\ \mathbf{Z_1'X} & \mathbf{Z_1'Z_1}+\alpha_1\mathbf{A^{-1}} & \mathbf{Z_1'Z_2} & \mathbf{Z_1'Z_2}+\alpha_2\mathbf{A^{-1}} \\ \mathbf{Z_2'X} & \mathbf{Z_2'Z_1} & \mathbf{Z_2'Z_2}+\alpha_3\mathbf{I} & \mathbf{Z_2'Z_2} \\ \mathbf{Z_2'X} & \mathbf{Z_2'Z_1}+\alpha_2\mathbf{A^{-1}} & \mathbf{Z_2'Z_2} & \mathbf{Z_2'Z_2}+\alpha_4\mathbf{A^{-1}} \end{bmatrix} \begin{bmatrix} \hat{\beta} \\ \hat{\mathbf{u}}_1 \\ \hat{\mathbf{u}}_2 \\ \hat{\mathbf{u}}_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X'y} \\ \mathbf{Z_1'y} \\ \mathbf{Z_2'y} \\ \mathbf{Z_2'y} \end{bmatrix}$$

where:

$$\alpha_1 = \frac{\sigma_e^2}{\sigma_A^2} \; ; \qquad \alpha_2 = \frac{\sigma_e^2}{\sigma_{AM}} \; ; \qquad \alpha_3 = \frac{\sigma_e^2}{\sigma_C^2} \; ; \qquad \alpha_4 = \frac{\sigma_e^2}{\sigma_M^2}$$

All known pedigree information was included in the analysis to reduce the effect of selection and to increase the accuracy of estimation through additional ties between animals (Meyer, 1993a,b). The pedigree information to build the **A** matrix included 138 sires and 1,349 dams. All sires in the data set and all cows in the first generation had unknown parents. As shown in Table 12, a total of 567 animals were considered as the base population. Genetic group for these animals was not included in the model because of the lack of information. Therefore, it was assumed that the difference

in genetic base is removed by including generation effect in the analyzed models.

Table 12. Distribution of sires and dams of calf through the four generations

Generation	No. of sires		No. of dams	
	Total	Unknown[a]	Total	Unknown[a]
1	37	37	315	315
2	41	41	344	20
3	33	33	340	25
4	27	27	350	69
Total	138	138	1349	429

[a]Number of sires or dams with unidentified parents

Likelihood ratio tests were used to determine the significance of the variance components for each trait. These tests involved comparing twice the difference in maximized restricted log likelihoods between two models, one of which was a nested subset of the other, not including the parameter of interest. This difference was then compared to a chi-square distribution with one degree of freedom. Based on these tests, the most appropriate univariate model was chosen for the multiple-trait analyses. Model 4 seemed to be the most appropriate model for this data set. Consequently, all multiple-trait analyses were carried out including direct and maternal additive genetic effects and their covariance. Due to the size of the data set and to restrict computational

requirements only pairwise trait analyses were considered. All analyses were carried out using the MTDFREML set of programs (Boldman et al., 1993). Convergence was considered to have been reached when the variance of -2log L in the simplex was less than 10^{-9} for univariate analyses and 10^{-6} for bivariate analyses. At least one restart was performed to make sure a global maximum had been reached.

Approximate standard errors for variance components and genetic parameters were obtained using the procedure suggested by Graser et al. (1987). Estimates of direct (h_A^2) and maternal (h_M^2) heritabilities were obtained as ratios of the additive direct and maternal additive variances to the phenotypic variance (σ_P^2), respectively. The proportion of the maternal permanent environmental variance to the σ_P^2 (p_c) was also calculated. The phenotypic variance was calculated as the sum of the direct and maternal genetic and the error variances and direct-maternal covariance components. Direct-maternal genetic correlation (r_{AM}) was estimated as the ratio of σ_{AM} to the square root of the product of σ_A^2 and σ_M^2. Total heritability (h_T^2) was estimated as follows (Willham, 1972): $h_T^2 = (\sigma_A^2 + 1.5\sigma_{AM} + 0.5\sigma_M^2)/\sigma_P^2$.

Results and Discussion

Likelihood ratio test statistics for BWT, WWT and ADG for each of the six models are presented in Table 13. The -2log L are given as -2 times the difference between the maximized restricted log L of model i and the most complete model

(Model 6). These differences were used to compare the significance of the corresponding variance components on preweaning growth traits. Estimates of variance-covariance components and genetic parameters are presented in Tables 14 to 19.

Direct and maternal factors affecting birth weight Table 13 shows the likelihood ratio test statistics for BWT for each of the six models. Differences in -2log L were used to compare the significance of the corresponding variance components on BWT. The -2log L values for BWT presented in Table 13 were consistent. Maternal permanent environmental variance seemed unimportant in explaining variation of BWT. This was evident when comparing -2log L values from either Models 1 and 2, Models 3 and 5, or Models 4 and 6. For any of these comparisons, the difference in -2log L was smaller than 3.84 (the critical chi-square value for one df and .05 type I error). Several papers have discussed the effect of maternal environmental variance on BWT (Meyer, 1992a, 1993a,b; Swalve, 1993; Waldron et al., 1993). Swalve (1993) and Waldron et al. (1993) reported similar results to those found in this study in at least one of the breeds they analyzed. Swalve (1993) found no effect of maternal environment on BWT of Simmental cattle, while Waldron et al. (1993) reported the same result for Hereford data.

Table 13. Likelihood ratio test statistics[a] obtained under Model 1-5 from the log likelihood under Model 6 for BWT, WWT and ADG

Model/Trait	BWT	WWT	ADG
1	85.95	95.66	106.92
2	85.95	95.66	106.92
3	3.69	10.31	22.89
4	.00	.00	.00
5	3.69	10.31	22.88

[a]-2 log likelihood expressed as deviation from "the most complete model" $[-2(\log L_i - \log L_6)]$

Estimates of variance-covariance components and genetic parameters for BWT for each of the six models are presented in Tables 14 and 15. Model 1 gave estimates of 16.24±1.36 for σ_A^2, 11.38 for σ_e^2 and .59±.04 for h_A^2. Including maternal environmental effects in the model (Model 2) did not change the estimates for σ_A^2 and h_A^2, but σ_e^2 decreased to 9.88 and maternal environment accounted for only 5% of the total variation of BWT. A similar pattern was found for the other models where maternal environmental effects were added. Thus, σ_A^2, σ_M^2, h_A^2 and h_M^2 were the same for Models 3 and 5 and for Models 4 and 6. Maternal environmental variance explained 8% of total variance of BWT in Model 5 and 7% of the total variance in Model 6. For all models including maternal environmental effect, σ_e^2 decreased compared to the models not containing this component. It seems that the σ_C^2

Table 14. Variance and covariance component estimates for BWT when fitting six different models

Model	σ^2_A	σ^2_M	σ_{AM}	σ^2_C	σ^2_e
1	16.24±1.36	-	-	-	11.38
2	16.23±1.37	-	-	1.50±19.87	9.88
3	11.50±1.50	4.44±0.66	-	-	11.45
4	9.48±1.55	3.76±0.68	1.58±0.72	-	12.49
5	11.50±1.57	4.44±0.65	-	2.26±0.77	9.19
6	9.47±1.72	3.75±0.68	1.58±0.74	1.87±6.10	10.62

Table 15. Estimates of genetic parameters for BWT when fitting six different models

Model	h^2_A	p_c	h^2_M	r_{AM}	h^2_T
1	.59±.04	-	-	-	.59
2	.59±.04	.05±.66	-	-	.59
3	.42±.05	-	.16±.02	-	.50
4	.35±.05	-	.14±.02	.26±.14	.50
5	.42±.05	.08±.15	.16±.02	-	.50
6	.35±.06	.07±.08	.14±.03	.27±.14	.50

was picked up by σ_c^2 when this effect was not included in the model such that there was some confounding between these two effects.

A similar value for h_A^2 was found by Meyer (1992a) in Hereford and Angus breeds when the animal effect was the only random effect in the model. Smaller values for h_A^2 than those found in this study were published by Meyer (1993b) and by Waldron et al. (1993). The latter authors found values for h_A^2 around .50, while Meyer (1993b) found a value of .25. All published values for h_A^2 from Model 2 were smaller than from Models 1 and 2 in this study. However, the published p_c are very close in magnitude to those reported in this study. They ranged from 5% in Charolais to 12% in Angus.

The direct heritabilities found in this study (h_A^2=.42±.05) for Models 3 and 5 were similar to those published by Meyer (1992a) in Hereford and Angus, and by Meyer (1993a) in Hereford. On the contrary, a much smaller h_A^2 of .20 was reported by Meyer (1993b) in Charolais cattle.

The direct heritability from Models 4 and 6 (h_A^2=.35±.05) was smaller than from Models 3 and 5. The same trend and magnitude were found by Meyer (1992a) in Hereford and Angus breeds. A larger value (h_A^2=.58) was published by Meyer (1993a) using Model 6, whereas Waldron et al. (1993) found smaller values than found in this study. These authors computed estimates of h_A^2 ranging from .23 to .33.

The maternal additive effect can be evaluated by comparing the log L values from either Models 1 and 3, or Models 2 and 5. Fitting a maternal additive genetic effect (Models 3 and 5) provided a better fit to the data. It increased values of log L markedly over those models not accounting for it (Models 1 and 2). A strong increase in log L value due to maternal additive variance was found in other papers (Meyer, 1992a, 1993a). On the contrary, Meyer (1993b) did not find an important effect of maternal genetic variance on BWT. Models 3 and 5 provided an estimate of σ_A^2 of 11.50±1.50, a reduction of about 30% compared to Model 1. The maternal heritability was .16±.02, whereas the estimate of direct heritability was reduced to .42±.05. Meyer (1992a, 1993a) found smaller values for h_M^2, ranging from .07 to .14. In these papers, the h_M^2 from Model 5 was always smaller than from Model 3.

Direct-maternal genetic covariance was small for BWT. For those models which included the direct-maternal covariance (Models 4 and 6), the -2log L value was 3.69 units smaller than models without σ_{AM} (Models 3 and 5) and tending toward statistical significance ($p<.06$). The estimate of σ_{AM} was 1.58±.72. Including σ_{AM} reduced the estimates of h_A^2 and h_M^2 so that the corresponding h_T^2 were the same. The direct-maternal genetic correlation in this study was .26±.14 from Model 4 and .27±.14 from Model 6. Larger values of r_{AM} for Model 6 than for Model 4 have been reported by Meyer (1992a)

and Waldron et al. (1993). A similar value for r_{AM} was found by Meyer (1992a) in Angus cattle, but she also found a r_{AM} close to zero in the Hereford herd. Waldron et al. (1993) found an average r_{AM} of .27 in Angus data, and a larger r_{AM} in the Hereford breed. They also reported a smaller r_{AM} in another Angus data set than the r_{AM} found in this study.

In conclusion, maternal permanent environmental effects added little to the explanation of BWT variability. Maternal additive genetic variance appeared to be extremely important in explaining the total variation of BWT, whereas the direct-maternal genetic covariance effect was small but still significant. Therefore, Model 4 provided the best fit to the BWT data.

Direct and maternal factors affecting weaning weight

Likelihood ratio test statistics for WWT are presented in Table 13. For WWT, fitting a maternal permanent environmental effect (Models 2, 5 and 6) did not increase the log L over models not including this effect (Models 1, 3 and 4). In fact, the differences in log L were equal to zero. This suggests that permanent environmental effects do not exist. Contrary to the findings in this study, all reviewed papers reported a significant increase in log L when maternal permanent environmental effects were considered. In a maternal animal model, the maternal environmental effect is modeled by the uncorrelated random effects of dam. Hence, it is a function of the number of records per dam. Data with

only a few records per dam increase the difficultly in separation of the maternal permanent environmental effect from the residual variance. The average progeny number per dam for this study was 2.90, which may be not large enough to give an accurate estimate of maternal variance. Consequently, σ_C^2 and σ_e^2 could be partially confounded.

Tables 16 and 17 display estimates of variance-covariance components and genetic parameters for WWT for each of the six models. Fitting a maternal environmental effect caused no change in the estimation of variance-covariance components, except σ_e^2 which decreased by the magnitude of σ_C^2. Meyer (1992a) reported a significant decrease in σ_A^2 when maternal permanent environmental effects were added to Model 1. The estimate of h_A^2 from Model 1 in this study (h_A^2=.54±.04) was larger than that reported by Meyer (1992a, 1993b), Mrode and Thompson (1990) and Waldron et al. (1993). In those studies, h_A^2 ranged from .12 to .44. The estimated p_e in this study was also much larger than in any other paper reviewed by the author. In fact, the maternal permanent environmental variance took away the whole residual variance, reducing σ_e^2 by 99%, reflecting the difficulty in separating these two effects.

Fitting a maternal genetic effect rather than a maternal environmental effect significantly increased the log L, suggesting a big contribution to the fit of the data. Except for Mrode and Thompson (1990) who did not find a significant

Table 16. Variance and covariance component estimates for WWT when fitting six different models

Model	σ_A^2	σ_M^2	σ_{am}	σ_C^2	σ_e^2
1	314.3±29.6	-	-	-	264.8
2	314.3±29.8	-	-	262.8±24.9	2.0
3	244.8±30.4	106.6±15.4	-	-	240.6
4	324.7±54.1	149.3±24.1	-78.48±29.9	-	197.8
5	244.6±30.4	106.5±15.4	-	2.1± 6.9	238.6
6	323.5±21.6	149.2±23.7	-78.22±34.6	46.1±52.8	152.2

Table 17. Estimates of genetic parameters for WWT when fitting six different models

Model	h_A^2	p_c	h_M^2	r_{AM}	h_T^2
1	.54±.04	-	-	-	.54
2	.54±.04	.45±.06	-	-	.54
3	.41±.04	-	.18±.02	-	.50
4	.55±.07	-	.25±.04	-.36±.09	.47
5	.41±.04	.00±.00	.18±.03	-	.50
6	.55±.04	.08±.02	.25±.05	-.36±.03	.47

effect of maternal genetic variance, all reviewed papers reported similar findings to those found in this study. The estimates for σ_A^2 and σ_M^2 from Model 3 were 244.8±30.4 and 106.6±15.4, respectively. The direct heritability was reduced to 41%, while the estimated h_M^2 was .18±.02. This h_A^2 was larger than those reported in the literature for Model 3 (Meyer, 1992a, 1993b; Mrode and Thompson, 1990). Nevertheless, the h_M^2 was very close to those reported by Meyer (1992a) in Angus and Zebu crosses and Meyer (1993b) in Charolais. But it was smaller than the value of .34 found by Meyer (1992a) in Hereford and much larger than the .07 reported by Mrode and Thompson (1990).

Including both maternal effects did not change the h_A^2, but p_c was reduced to zero. The estimated σ_c^2 was very similar to that found for Models 3 and 1. All the reviewed papers reported a decrease in p_c for Model 5 but not as large as was found in this study. Published papers did not detect a change in h_A^2 when switching from Model 3 to Model 5, but reported a reduction in h_M^2 (Meyer, 1992a, 1993b).

The direct-maternal covariance significantly contributed to a better fit of the data. Compared to Model 3, the -2log L was reduced by about 10.31 units ($p<.05$). Both h_A^2 and h_M^2 increased, pointing toward some cross-substitution effect in partitioning of the total variation when estimating highly correlated parameters (Meyer, 1992a). Sampling correlations of -.74 between σ_A^2 and σ_{AM} and -.74 between σ_M^2 and σ_{AM} were

found in this study under Model 4 (see Table 28 in Appendix). The same tendency was found by Meyer (1992a) in Hereford and Zebu crosses but it was the opposite in Angus cattle. The direct-maternal genetic correlation found in this study was -.36±.09, which was accompanied by an increase in estimates of both direct and maternal heritabilities and a slight reduction in total heritability. This value did not change when maternal environment was added to the model (Model 6). In the papers by Meyer (1992a, 1993b) and by Waldron et al. (1993) similar findings were reported. However, Meyer (1992a) reported a positive value for r_{AM} in Angus and Waldron et al. (1993) found a small but positive value for r_{AM} in one Angus herd and zero in the other Angus herd. Other reviewed papers found larger negative values than the found in this study. The p_c from Model 6 in the present study was .08±.02, which is smaller than that found by Meyer (1992a) for Hereford and Zebu crosses but larger than the value for Angus. Meyer (1993a,b) and Waldron et al. (1993) also reported larger values for this parameter.

According to the changes in log L and genetic parameters determined in this study, it seems that the most appropriate model for weaning weight was Model 4. Other than the direct additive animal effect, maternal additive variance and the direct-maternal additive covariance should be considered in evaluating weaning weight.

Direct and maternal factors affecting preweaning average daily gain Variance-covariance components and genetic parameters for each of the six models are shown in Tables 18 and 19. The random factors affecting ADG were the same as those influencing both BWT and WWT. As log L values clearly show, as for BWT and WWT, maternal effects on ADG in this data set were entirely genetic. The log L values did not increase when fitting maternal permanent environmental variance into the model. On the other hand, maternal additive genetic effects affected the estimates of all genetic parameters under the model in question. The variance component for maternal environment was almost zero for all models, whereas the maternal additive genetic effect accounted for 18% when direct-maternal covariance was not fitted and 30% when the covariance was fitted.

Including a direct-maternal covariance (Models 4 and 6) yielded a large negative estimate for r_{AM} (-.49±.08) while increasing estimates of both h_A^2 and h_M^2 (from .38 to .57 for h_A^2 and from .18 to .30 for h_M^2). Although a large increase in direct and maternal heritability was found when σ_{AM} was added, the large negative value for r_{AM} caused a reduction of about 13% in h_T^2. As for WWT, a cross-substitution effect seemed to be present. The sampling correlation between σ_A^2 and σ_{AM} was -.77 and between σ_M^2 and σ_{AM} was -.79. In conclusion, the model allowing for both maternal genetic and direct-maternal covariance provided the best fit to the data.

Table 18. Variance and covariance component estimates for ADG when fitting six different models

Model	σ^2_A	σ^2_M	σ_{AM}	σ^2_C	σ^2_e
1	.0056±.0006	-	-	-	.00585
2	.0056±.0006	-	-	.0001±.0004	.00581
3	.0044±.0006	.0021±.0003	-	-	.00521
4	.0067±.0011	.0036±.0005	-.0024±.0007	-	.00397
5	.0044±.0006	.0021±.0003	-	.0001±.0009	.00514
6	.0067±.0012	.0036±.0005	-.0024±.0007	.0000±.0005	.00394

Table 19. Estimates of genetic parameters for ADG when fitting six different models

Model	h^2_A	p_c	h^2_M	r_{AM}	h^2_T
1	.49±.04	-	-	-	.49
2	.49±.04	.00±.08	-	-	.49
3	.38±.04	-	.18±.02	-	.47
4	.57±.08	-	.30±.04	-.49±.08	.41
5	.38±.04	.01±.04	.18±.02	-	.47
6	.57±.08	.00±.01	.30±.04	-.49±.08	.41

Direct and maternal genetic parameters for preweaning growth traits Univariate estimates of direct and maternal heritabilities and direct-maternal genetic correlations for BWT, WWT and ADG under the "best" model (Model 4) are presented in Table 20. Bivariate estimates of the same parameters are given in Table 21. In general, the univariate estimates were the same as the bivariate estimates. This has been a norm for all published papers except the one by Mackinnon et al. (1991) who found that the multivariate estimates of h_A^2 for BWT and WWT were much larger than the corresponding univariate estimates. However, they pointed out that their estimates were inflated by maternal effects since they were not included in the model. Results from the two bivariate analyses (i.e., BWT-WWT and BWT-ADG) agreed well. Some small fluctuations were observed, probably due to the effects of sampling variation on the accuracy of partitioning direct and maternal and genetic and environmental effects (Meyer, 1993a). In addition, the additive genetic correlation between ADG and WWT frequently converged to the bound of the parameter space during the iteration process. However, it did not affect the estimation of the other parameters even when it was fixed to 1.0. Therefore, the following discussion will be based on bivariate estimates.

Table 20. Univariate estimates of genetic parameters and their approximate standard error for BWT, WWT and ADG under the "best" model (Model 4)

Model	h_A^2	h_M^2	r_{AM}	h_T^2
BWT	.35±.05	.14±.02	.26±.14	.51
WWT	.55±.07	.25±.04	-.36±.09	.47
ADG	.57±.08	.30±.04	-.49±.08	.42

The estimate of direct heritability for BWT (h_A^2=.36) was in close agreement with the average value of the literature survey summarized by Koots et al. (1991) and Meyer (1992a) but slightly higher than that summarized by Mohiuddin (1993). On the contrary, the estimates of h_A^2 for WWT and ADG (h_A^2=.54 for WWT and h_A^2=.56 for ADG) were quite high. They were much larger than average values summarized by Koots et al. (1991), Meyer (1992a) and Mohiuddin (1993). In the summary by Meyer (1992a), the corresponding values of h_A^2 for BWT, WWT and ADG were .36, .25 and .32, respectively. Koots et al. (1991) and Mohiuddin (1993) reported mean values of .34 and .30 for BWT and .26 and .22 for WWT, respectively.

Estimates of h_A^2 for preweaning growth traits in the literature are quite variable. This could be due to different methods of estimation, statistical models and population variability where this parameter has been estimated. Brown et al. (1990) reported heritability estimates for direct additive effects of .63 and .66 for WWT

Table 21. Estimates of (co)variance components and genetic parameters from bivariate analyses of BWT, WWT and ADG using Model 4

	BWT +		WWT +		ADG +	
	WWT	ADG	BWT	ADG	BWT	WWT
σ^2_A	9.99	10.05	325.81	326.66	.0066	.0067
σ^2_M	3.77	3.79	171.22	154.08	.0037	.0035
σ_{AM}	1.58	1.56	-88.48	-84.99	-.0024	-.0024
σ^2_e	12.19	12.15	204.62	198.67	.0040	.0040
σ^2_P	27.53	27.56	613.16	594.43	.0120	.0118
σ_A	25.26	-	-	1.46	.0748	-
σ_M	8.62	-	-	-	.0230	.7265
σ_{A1M2}	10.59	-	-	-	.0238	-.4593
σ_{A2M1}	6.38	-	-	-	.0438	-.4421
σ_e	25.30	-	-	-	.0642	.8728
σ_P	67.67	-	-	2.60	.1959	-
h^2_A	.36	.36	.53	.55	.5500	.5700
h^2_M	.14	.14	.28	.26	.3100	.2900
r_{AM}	.26	.25	-.37	-.38	-.4800	-.4900
r_A	.44	.29	-	.98	-	-
r_M	.34	.19	-	.99	-	-
r_{A1M2}	.26	.23	-	-.41	-	-
r_{A2M1}	.18	.15	-	-.45	-	-
r_e	.51	.29	-	.98	-	-

σ_A, direct additive genetic covariance; σ_M, maternal additive genetic covariance; σ_e, residual covariance; r_A, direct additive genetic correlation; r_M, maternal additive genetic correlation; r_e, residual correlation

for Angus and Hereford, respectively. Meyer (1992a) found a h_A^2 of .58 for WWT for Zebu crosses. These are the only two h_A^2 estimates in the literature that are larger than or equal to values found in this study. Estimates of h_A^2 for WWT (using sire-maternal grandsire models) smaller than .54 were reported by Quaas et al. (1985), Bertrand and Benyshek (1987), Garrick et al. (1989) and Shi et al. (1993). Smaller values for h_A^2 were also reported using a maternal animal model (Kriese et al., 1991; Mackinnon et al., 1991; Meyer, 1992a, 1993a,b; Arthur et al., 1994; Lobo et al., 1994). Mrode and Thompson (1990), Swalve (1993), Waldron et al. (1993) and Pang et al. (1994) also reported h_A^2 for WWT smaller than .54.

The direct heritability for BWT found in this study was very close to those reported in the literature (Trus and Wilton, 1988; Kriese et al., 1991, in Brahman; Meyer, 1992a; Shi et al., 1993; Waldron et al., 1993, in Angus). Others (Burfening et al., 1981; Quaas et al., 1985; Bertrand and Benyshek, 1987; Trus and Wilton, 1988, in Shorthorn; Kriese et al., 1991, in Brangus; Meyer, 1993b; Waldron et al., 1993, in Hereford; Lobo et al., 1994) reported a h_A^2 smaller than .36. Larger values were reported by Garrick et al. (1989), Brown et al. (1990), Mackinnon et al. (1991), Meyer (1993a), Swalve (1993), Arthur et al. (1994) and Pang et al. (1994). The estimated direct heritability for ADG in this study was smaller than that reported by Brown et al. (1990) but larger than the values found by Mackinnon et al. (1991), Trus and

Wilton (1988) and Shi et al. (1993). The values reported by these authors ranged from .16 to .43. Most of the heritability estimates that have been published were based on purebred cattle. It is known that crossbreeding increases genetic variation due to gene frequency differences among the original pure breeds. This could be one reason for the larger h_A^2 for ADG and WWT found in this study. Another reason mentioned by Wright et al. (1987) is that analyses of data collected at experiment or research stations produce heritabilities larger than estimates from field data.

As expected, maternal heritabilities were lower than direct heritabilities for all three traits, implying that preweaning growth traits were determined more by genetic characteristics of the calf than those of the dam. Weaning weight and preweaning gain were more influenced by direct and maternal genetic effects than BWT. The same trend is reported in the literature for BWT and WWT (see Tables 3 and 4). Mackinnon et al. (1991), Waldron et al. (1993) in Angus and Pang et al. (1994) reported estimates of h_M^2 for WWT larger than the corresponding estimates of h_A^2. All other reviewed papers found larger estimates for h_A^2 (see Tables 3 and 4). Estimates of h_M^2 in the literature ranged from .04 to .22 for BWT, .04 to .76 for WWT and .13 to .39 for ADG. The estimates in this study were .14, .27 and .30 for BWT, WWT and ADG, respectively. In the literature summary by Meyer (1992a), the average values of h_M^2 were .17 for BWT, .20 for

WWT and .23 for ADG. Mohiuddin (1993) also summarized literature results. He found .10 and .13 as the average values of h^2_M for BWT and WWT, respectively. Koots et al. (1991) reported average values of .18 and .21 for the h^2_M for BWT and WWT from a different set of published papers. It is reasonable to expect a larger maternal influence on WWT and ADG than on BWT since the former two traits can reflect the maternal intrauterine environment in addition to the maternal influence from birth to weaning. Hohenboken (1985) said that the dam may influence offspring phenotype through the quality and quantity of protection that she provides, through modification of offspring behavior mediated by her own behavior and by the quantity and/or quality provided through the milk.

Burfening et al. (1981), Bertrand and Benyshek (1987) in Brangus, Garrick et al. (1989), Trus and Wilton (1988) in Angus, Hereford and Charolais, Kriese et al. (1991) in Brangus, Mackinnon et al. (1991) and Waldron et al. (1993) in Hereford reported h^2_M for BWT ranging from .11 to .17. Others (Trus and Wilton, 1988 in Shorthorn and Charolais; Brown et al., 1990; Kriese et al., 1991 in Brahman; Meyer, 1993a; Arthur et al., 1994; Pang et al., 1994) found larger h^2_M for BWT than reported in this study. Smaller values were reported by Quaas et al. (1985), Bertrand and Benyshek (1987) in Limousin, Meyer (1992a), Shi et al. (1993), Swalve (1993) and Waldron et al. (1993) in Angus. The total heritability

of BWT was .52, suggesting that simultaneous selection for direct and maternal effects can be effective in changing this trait.

The maternal heritability for WWT found in this study is smaller than the value reported by Brown et al. (1990) in Hereford, Mackinnon et al. (1991), Meyer (1992a) in Zebu crosses, Arthur et al. (1994) and Pang et al. (1994) but larger than the h_M^2 reported by Bertrand and Benyshek (1987), Garrick et al. (1989), Brown et al. (1990) in Angus, and Kriese et al. (1991). It is also larger than the value from Quaas et al. (1985), Meyer (1992a) in Hereford and Angus, Meyer (1993a,b), Shi et al. (1993), Swalve (1993) and Waldron et al. (1993). The h_M^2 for ADG in this study is in close agreement to that reported by Trus and Wilton (1988) in Hereford and Shorthorn and Mackinnon et al. (1991). Brown et al. (1990) in Hereford reported a larger value, while Trus and Wilton (1988) in Angus, Charolais and Simmental, Brown et al. (1990) in Hereford and Shi et al. (1993) reported smaller values than the found in this study. Of the potential causes of maternal effects, milk is assumed to be the most important (Hohenboken, 1985). Gleddie and Berg (1968) and Hohenboken et al. (1973) have documented the association between milk production of the dam and progeny preweaning growth in beef cattle. This correlation was larger than .70.

Birth weight was the only trait having a positive direct-maternal genetic covariance. Similar values in sign and size

to the r_{AM} of BWT found in this study have been reported by Meyer (1992a) in Angus and Waldron et al. (1993) in Hereford and Angus. Positive r_{AM} but smaller than .25 were reported by Mackinnon et al. (1991), Meyer (1992a) in Hereford and Waldron et al. (1993) in Angus. However, larger estimates were found by Quaas et al. (1985), Trus and Wilton (1988) in Shorthorn and Swalve (1993). Estimates of r_{AM} for BWT between -.20 and -.30 were reported by Burfening et al. (1981) and Trus and Wilton (1988) in Simmental; larger negative estimates were reported by Trus and Wilton (1988) in Angus, Hereford and Charolais, Garrick et al. (1989), Kriese et al. (1991) in Brangus, Meyer (1993a), Shi et al. (1993) and by Arthur et al. (1994). Other papers have reported estimates of r_{AM} for BWT between -.11 and -.20 (Bertrand and Benyshek, 1987; Brown et al., 1990; Kriese et al., 1991 in Brahman; Pang et al., 1994).

The r_{AM} for ADG in this study was -.48, which is close to the value reported by Trus and Wilton (1988) in Angus and Simmental. Negative, but smaller values (in absolute terms) than that found in this study were reported by Trus and Wilton (1988) in Hereford, Shorthorn and Charolais, Brown et al. (1990) and Shi et al. (1993). Mackinnon et al. (1991) reported a null value for r_{AM} of ADG.

The estimated direct-maternal genetic correlation of WWT in this study was -.37. Robison (1981) mentioned that progeny of dams producing little milk are forced to seek

supplemental feed earlier which may over-compensate for the extra milk produced by other dams. This factor may contribute to a more negative estimate of r_{AM} for ADG and WWT. This value agrees with the value found by Garrick et al. (1989), Brown et al. (1990) in Angus, Meyer (1993a) and Waldron et al. (1993) in Hereford. Estimates of r_{AM} ranging from -.59 to -.99 have been reported (Meyer, 1992a in Hereford and Zebu crosses; Swalve, 1993; Arthur et al., 1994; Pang et al., 1994). Smaller negative values than that found in this study were also reported in the literature (Quaas et al., 1985; Bertrand and Benyshek, 1987; Brown et al., 1990 in Hereford; Kriese et al., 1991 in Brangus). However, positive direct-maternal genetic correlations for WWT were also reported (Kriese et al., 1991 in Brahman; Meyer, 1992a in Angus and Waldron et al., 1993 in Angus).

These negative direct-maternal genetic correlations for WWT and ADG indicate an antagonistic genetic relationship between growth and milk, suggesting that the loss in maternal performance due to intense selection for direct ADG or WWT is potentially large. On the other hand, caution must be taken in interpreting the r_{AM} from Model 4 since dam-daughter environmental covariance was assumed to be zero in this study. There have been concerns about a negative maternal environmental dam-daughter covariance that, if ignored, is likely to bias estimates of the other components and corresponding genetic parameters, in particular r_{AM} (Willham,

1980; Koch, 1972; Cantet et al., 1988; Meyer, 1992b). This negative relationship between early growth rate and subsequent maternal ability of beef cows has been documented in the literature (Christian et al., 1965; Mangus and Brinks, 1971; Koch, 1972). Johnsson and Morant (1984), using field data, found a negative relationship between weaning weights of beef heifers and weaning weights of their first calves, meaning that daughters of dams with superior maternal abilities may provide an inferior maternal environment for their offspring.

Baker (1980), cited by Meyer (1992a), documented the possible bias of r_{AM} due to dam-daughter environmental covariance. Based on published papers, he found r_{AM} of -.42, -.45 and -.72 for BWT, ADG and WWT, respectively, considering information from the dam-offspring covariance and of .00, -.05 and -.07 excluding dam-offspring covariance. Another factor that might be disturbing the estimate from maternal models is that relatively large sampling variances of the estimates could exist for maternally influenced traits (Thompson, 1976; Meyer, 1992b).

All three traits analyzed in this study are heritable enough to allow selection for direct genetic effects. However, this could result in deterioration of the maternal ability because of the negative direct-maternal genetic correlation, particularly if such selection is applied on WWT or ADG.

Variance-covariance components and genetic and environmental correlations among preweaning growth traits are given in Table 21. The direct additive genetic correlations (r_A) were positive, suggesting that animals that are genetically superior for the direct effect of one trait (i.e., WWT) are also, on average, genetically superior for the direct effect of the other traits. The r_A between BWT and WWT was .44, thus almost identical with the literature averages given by Koots et al. (1991) but smaller than the mean value summarized by Mohiuddin (1993). Koots et al. (1991) reported .46 while Mohiuddin (1993) found .63 as the average value. Quaas et al. (1985) reported a r_A of .43 and Garrick et al. (1989) reported a value of .49; both papers used sire-grandsire models on Simmental data. In comparison, values larger than those found in this study have been published (Mackinnon et al., 1991; Meyer, 1993a,b; Swalve, 1993). Meyer (1993a,b) reported a r_A of .56, whereas Mackinnon et al. (1991) reported .57 and Swalve (1993) reported .59 as the r_A between BWT and WWT. The r_A between BWT and ADG was .29, which is close to the .36 reported by Mackinnon et al. (1991). The same correlation between WWT and ADG was .98, which is also very close to the estimated r_A of Mackinnon et al. (1991). They found a r_A of .94. The same genes tend to influence WWT and ADG; selection for one will improve the other as a correlated response. Higher weaning weight will generally be associated with higher preweaning gain.

Maternal genetic correlations (r_M) were .34, .19 and .99 between BWT and WWT, BWT and ADG and WWT and ADG, respectively. The r_M between BWT and WWT agrees with the literature average of .33 given by Koots et al. (1991) and smaller than the value of .42 reported by Garrick et al. (1989) and the value of .53 found by Swalve (1993). Smaller values than estimated in this study for BWT and WWT were reported by Quaas et al. (1985) and Meyer (1993a), which were .26 and .14, respectively. These positive maternal correlations seem to indicate that these traits are under the influence of similar genes, particularly WWT and ADG. Genetic change in one trait is expected to accompany a change in the other.

The genetic correlation between direct BWT and maternal WWT effects was .26, which is much larger than any other estimate in the literature. This correlation ranged from -.03 to -.23 (Quaas et al., 1985; Garrick et al., 1989; Meyer, 1993a; Swalve, 1993). The mean value from published papers was -.12 (Koots et al., 1991). The genetic correlation between maternal BWT and direct WWT effect was also positive (.18). Except for Swalve (1993) who found a value of -.24, all other papers reported negative values but very close to zero (Quaas et al., 1985; Garrick et al., 1989; Meyer, 1993a). Koots et al. (1991) reported a value of -.07 as the maternal BWT-direct WWT mean correlation from published papers. The direct BWT and maternal ADG genetic correlation

was .23, while the maternal BWT and direct ADG correlation was .15. Weaning weight and average daily gain had a negative direct-maternal genetic correlation. The direct WWT - maternal ADG correlation was -.41 and the genetic correlation was -.45 between maternal WWT and direct ADG.

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CHAPTER III

ADDITIVE AND NONADDITIVE GENETIC EFFECTS FOR PREWEANING GROWTH TRAITS OF CROSSBRED CATTLE

Introduction

Crossbreeding is a very useful tool for improving production efficiency of commercial beef cattle (Franke, 1980; Turner, 1980; Cunningham and Magee, 1988). Knowledge of breed additive and heterotic genetic effects are important in designing effective crossbreeding systems for beef cattle production. Gregory et al. (1980) pointed out that crossbreeding provides a way to use both nonadditive (heterosis) and additive (breed differences) effects of genes simultaneously. Therefore, an evaluation of direct, maternal and non-additive genetic effects of individual breeds is necessary to choose the appropriate breeds and the manner of combining them in a crossbreeding system.

Estimates of breed direct and maternal genetic and heterotic effects for different traits have been obtained by linear functions of least-squares breed group means from statistical models ignoring random sire effects (Gregory et al., 1978; Alenda et al., 1980), following a method originally described by Dickerson (1973). Other authors (Dillard et al., 1980; Robison et al., 1981; Peacock et al., 1982; Marshall et al., 1987; Thorpe et al., 1993) have used a multiple regression approach to estimate breed direct and maternal genetic and heterotic effects in a fixed model not

including sire effects. More recently, sire effect was included in the papers by Comerford et al. (1988), DeRouen et al. (1992), and Morris et al. (1994), but sires were considered unrelated. Therefore, the objectives of this study were:

1. To estimate breed direct and maternal additive genetic effects for the Angus, Brahman, Charolais, and Hereford using a maternal animal model.
2. To estimate direct and maternal heterotic genetic effects for the Angus, Brahman, Charolais, and Hereford using a maternal animal model.

Materials and Methods

Source of data Pre-weaning growth trait records for this study came from four generations of a long-term rotational crossbreeding study conducted at the Ben Hur Beef Cattle Crossbreeding Unit of the Louisiana Agricultural Experiment Station, Baton Rouge, Louisiana. Baton Rouge is located at latitude 30°31′ N and longitude 91°08′ W and is 10.8 m above sea level. The climate is subtropical with average daily minimum and maximum temperature of 18 and 26 °C, average daily minimum and maximum humidity of 45 and 88%, and average annual rainfall of 147 cm (LAIS, 1989).

This crossbreeding experiment included four straightbred and seven rotational crossbred lines. The four straightbred lines used as controls were Angus (A), Brahman (B), Charolais

(C) and Hereford (H). The crossbred lines were the three two-breed (A-B, C-B and H-B), three three-breed (A-B-C, A-B-H, and B-C-H), and one four-breed (A-B-C-H) rotational mating system combinations that included B. These crossbred lines were initiated with F_1 A-B, C-B and H-B cows in generation one. The mating scheme and expected breed composition per generation is shown in Table 22. Each generation lasted for four years with no overlapping.

Variables used in this study included generation, calf year of birth, calf julian birthdate, cow line, cow breed, calf weaning age, sex of calf, calf breed, cow age at parturition, and sire, cow and calf identification. A total of 16 years was uniformly distributed through the four generations. Age of cow at parturition ranged from two to 18 years. Pre-weaning growth traits of interest were birth weight (BWT), weaning weight (WWT) and average daily gain (ADG). Birth weight and weaning weight were adjusted to a male and mature cow basis before analysis. In addition, weaning weight was adjusted to 205 d weaning age. The adjustment factors were those recommended by BIF (1990). Individual average daily gain from birth to weaning was calculated using the adjusted birth and weaning weights. Data and pedigree information used in this analysis spanned years of birth from 1970 to 1988. Management of cattle was the same as presented in Chapter II.

Table 22. Expected breed composition for generations one to four for each line

Line	Generation 1	2	3	4
Straightbreds				
Angus	A	A	A	A
Brahman	B	B	B	B
Charolais	C	C	C	C
Hereford	H	H	H	H
Two-breed rotations[a]				
AB	A_3B_1	B_5A_3	$A_{11}B_5$	$B_{21}A_{11}$
CB	C_3B_1	B_5C_3	$C_{11}B_5$	$B_{21}C_{11}$
HB	H_3B_1	B_5H_3	$H_{11}B_5$	$B_{21}H_{11}$
Three-breed rotations				
ABC	$C_2A_1B_1$	$A_5C_2B_1$	$B_9A_5C_2$	$C_{18}B_9A_5$
ABH	$A_2H_1B_1$	$H_5A_2B_1$	$B_9H_5A_2$	$A_{18}B_9H_5$
BCH	$C_2H_1B_1$	$H_5C_2B_1$	$B_9H_5C_2$	$C_{18}B_9H_5$
Four-breed rotations				
ABCH	$H_2A_1B_1$	$C_4H_2A_1B_1$	$B_9C_4H_2A_1$	$A_{17}B_9C_4H_2$

[a]Subscripts represent proportion of breeding of specific breeds. Example A_3B_1 represents 3/4 Angus and 1/4 Brahman

Statistical analysis A multiple regression analysis suggested by Koger et al. (1975) was used to partition calf preweaning data into breed-direct, breed-maternal, individual heterosis and maternal heterosis effects. Similar procedures have been used by Wyatt and Franke (1986), Elzo et al. (1990) and Olson et al. (1993). The genetic model is as follows (Model 7):

$$C_{lm} = \mu + \Sigma f_l g_l^I + \Sigma f_m g_m^I + \Sigma f_m' g_m^M + \Sigma f_{lm} h_{lm}^I + \Sigma f_{lm} h_{lm}^M + \epsilon$$

where

C_{lm} = the lm^{th} cross;

μ = the overall genetic mean;

f_l, f_m = the fractions of genes in the progeny contributed by the l^{th} breed through the sire and m^{th} breed through the dam;

g_l^I, g_m^I = the direct additive genetic effect expressed in individuals of the l^{th} and m^{th} breeds;

f_m' = the fraction of genes in dams from the breed m;

g_m^M = the maternal dam additive genetic effect of the m^{th} breed;

f_{lm} = the fraction of loci with one gene from one breed and the other gene from a different breed in individuals and dams;

h_{lm}^I, h_{lm}^M = the individual and maternal heterosis effects; and

ϵ = the residual error.

The incidence matrix for Model 7 results in a singular matrix, since $f_A + f_B + f_H + f_C = f'_A + f'_B + f'_C + f'_H = 1$. Therefore, it was necessary to impose certain restrictions. By omitting coefficient columns associated with direct and maternal additive effects of the Hereford breed from the incidence matrix, the remaining breed direct and maternal additive effects are computed as deviations from the Hereford breed (Wyatt and Franke, 1986). Based on results from Chapter II, a modification of Model 4 was used to estimate the multiple regression coefficients. Model 4 was modified by redefining line effects in terms of additive and nonadditive genetic effects. Bivariate analysis were evaluated using the following model (Model 8):

$$\begin{aligned} Y_{ijk} = \mu + G_i + a_j + m_k + b_1(Year_{ijk} - \overline{Year}) + \\ b_2(Year_{ijk} - \overline{Year})^2 + b_3(JBD_{ijk} - \overline{JBD}) + \\ b_4(JBD_{ijk} - \overline{JBD})^2 + f_A g^I_A + f_B g^I_B + f_C g^I_C + \\ f'_A g^M_A + f'_B g^M_B + f'_C g^M_C + f_{AB} h^I_{AB} + \\ f_{AC} h^I_{AC} + f_{AH} h^I_{AH} + f_{BC} h^I_{BC} + f_{BH} h^I_{BH} + \\ f_{CH} h^I_{CH} + f'_{AB} h^M_{AB} + f'_{AC} h^M_{AC} + f'_{AH} h^M_{AH} + \\ f'_{BC} h^M_{BC} + f'_{BH} h^M_{BH} + f'_{CH} h^M_{CH} + \epsilon_{ijk} \end{aligned}$$

where

Y_{ijk} = the BWT, WWT or ADG record for animal k;

G_i = the fixed effect of the i^{th} generation;

a_j = the random direct additive effect of animal j;

m_k = the random maternal additive effect of k^{th} dam;

Year = the year of birth of animal j;

$\overline{Year}$ = the mean calf birth year;

JBD = the julian birthdate of animal j;

$\overline{JBD}$ = the mean julian birthdate;

b_1, b_2 = the linear and quadratic regression coefficients of Y on year;

b_3, b_4 = the linear and quadratic regression coefficients of Y on julian birthdate;

g's, h's = the genetic effects defined previously;

f's = coefficients of the genetic effects; and

ϵ_{ijk} = the residual error.

The coefficients of the genetic effects (f's) were obtained by determining the fraction of genes attributable to a specific breed type based on the procedures developed by Dillard et al. (1980), Neville et al. (1984b), and Wyatt and Franke (1986). The fractional coefficients for genetic effects of the different breed groups are shown in Tables 23 and 24. Solutions under Model 8 were computed using the MTDFREML set of programs (Boldman et al., 1993). The variance-covariance components previously estimated (Chapter II) were used as the genetic and environmental matrices. The corresponding genetic effects and their respective standard errors were estimated as the average of the two bivariate analyses. These estimated coefficients were used to make contrasts among genetic effects. Approximate tests for significance of contrast were conducted. If the standard

Table 23. Coefficients used for estimation of breed-direct and heterotic-direct genetic effects for preweaning growth traits of beef cattle

Calf breed Group	Coefficients for genetic effects									
	f_A	f_B	f_C	f_H	f_{AB}	f_{AC}	f_{AH}	f_{BC}	f_{BH}	f_{CH}
A	1	0	0	0	0	0	0	0	0	0
B	0	1	0	0	0	0	0	0	0	0
C	0	0	1	0	0	0	0	0	0	0
H	0	0	0	1	0	0	0	0	0	0
A_1B_1	1/2	1/2	0	0	1	0	0	0	0	0
C_1B_1	0	1/2	1/2	0	0	0	0	1	0	0
H_1B_1	0	1/2	0	1/2	0	0	0	0	1	0
A_3B_1	3/4	1/4	0	0	1/2	0	0	0	0	0
C_3B_1	0	1/4	3/4	0	0	0	0	1/2	0	0
H_3B_1	0	1/4	0	3/4	0	0	0	0	1/2	0
B_5A_3	3/8	5/8	0	0	3/4	0	0	0	0	0
B_5C_3	0	5/8	3/8	0	0	0	0	3/4	0	0
B_5H_3	0	5/8	0	3/8	0	0	0	0	3/4	0
$A_{11}B_5$	11/16	5/16	0	0	5/8	0	0	0	0	0
$C_{11}B_5$	0	5/16	11/16	0	0	0	0	5/8	0	0
$H_{11}B_5$	0	5/16	0	11/16	0	0	0	0	5/8	0
$B_{21}A_{11}$	11/32	21/32	0	0	11/16	0	0	0	0	0

(table con'd)

Calf breed Group	Coefficients for genetic effects									
	f_A	f_B	f_C	f_H	f_{AB}	f_{AC}	f_{AH}	f_{BC}	f_{BH}	f_{CH}
$B_{21}C_{11}$	0	21/32	11/32	0	0	0	0	11/16	0	0
$B_{21}H_{11}$	0	21/32	0	11/32	0	0	0	0	11/16	0
$C_2A_1B_1$	1/4	1/4	1/2	0	0	1/2	0	1/2	0	0
$A_2H_1B_1$	1/2	1/4	0	1/4	1/2	0	1/2	0	0	0
$C_2H_1B_1$	0	1/4	1/2	1/4	0	0	0	1/2	0	1/2
$A_5C_2B_1$	5/8	1/8	1/4	0	1/4	1/2	0	0	0	0
$H_5A_2B_1$	1/4	1/8	0	5/8	0	0	1/2	0	1/4	0
$H_5C_2B_1$	0	1/8	1/4	5/8	0	0	0	0	1/4	1/2
$B_9A_5C_2$	5/16	9/16	1/8	0	5/8	0	0	1/4	0	0
$B_9H_5A_2$	1/8	9/16	0	5/16	1/4	0	0	0	5/8	0
$B_9H_5C_2$	0	9/16	1/8	5/16	0	0	0	1/4	5/8	0
$C_{18}B_9A_5$	5/32	9/32	9/16	0	0	5/16	0	9/16	0	0
$A_{18}B_9H_5$	9/16	9/32	0	5/32	9/16	0	5/16	0	0	0
$C_{18}B_9H_5$	0	9/32	9/16	5/32	0	0	0	9/16	0	5/16
$H_2A_1B_1$	1/4	1/4	0	1/2	0	0	1/2	0	1/2	0
$C_4H_2A_1B_1$	1/8	1/8	1/2	1/4	0	1/4	0	1/4	0	1/2
$B_9C_4H_2A_1$	1/16	9/16	1/4	1/8	1/8	0	0	1/2	1/4	0
$A_{17}B_9C_4H_2$	17/32	9/32	1/8	1/16	9/16	1/4	1/8	0	0	0

Table 24. Coefficients used for estimation of maternal additive and heterotic genetic effects for preweaning growth traits of beef cattle

Dam breed Group	Coefficients for genetic effects									
	f_A	f_B	f_C	f_H	f_{AB}	f_{AC}	f_{AH}	f_{BC}	f_{BH}	f_{CH}
A	1	0	0	0	0	0	0	0	0	0
B	0	1	0	0	0	0	0	0	0	0
C	0	0	1	0	0	0	0	0	0	0
H	0	0	0	1	0	0	0	0	0	0
A_1B_1	1/2	1/2	0	0	1	0	0	0	0	0
C_1B_1	0	1/2	1/2	0	0	0	0	1	0	0
H_1B_1	0	1/2	0	1/2	0	0	0	0	1	0
A_3B_1	3/4	1/4	0	0	1/2	0	0	0	0	0
C_3B_1	0	1/4	3/4	0	0	0	0	1/2	0	0
H_3B_1	0	1/4	0	3/4	0	0	0	0	1/2	0
B_5A_3	3/8	5/8	0	0	3/4	0	0	0	0	0
B_5C_3	0	5/8	3/8	0	0	0	0	3/4	0	0
B_5H_3	0	5/8	0	3/8	0	0	0	0	3/4	0
$A_{11}B_5$	11/16	5/16	0	0	5/8	0	0	0	0	0
$C_{11}B_5$	0	5/16	11/16	0	0	0	0	5/8	0	0

(table con'd)

Calf breed Group	Coefficients for genetic effects									
	f_A	f_B	f_C	f_H	f_{AB}	f_{AC}	f_{AH}	f_{BC}	f_{BH}	f_{CH}
$H_{11}B_5$	0	5/16	0	11/16	0	0	0	0	5/8	0
$C_2A_1B_1$	1/4	1/4	1/2	0	0	1/2	0	1/2	0	0
$A_2H_1B_1$	1/2	1/4	0	1/4	1/2	0	1/2	0	0	0
$C_2H_1B_1$	0	1/4	1/2	1/4	0	0	0	1/2	0	1/2
$A_5C_2B_1$	5/8	1/8	1/4	0	1/4	1/2	0	0	0	0
$H_5A_2B_1$	1/4	1/8	0	5/8	0	0	1/2	0	1/4	0
$H_5C_2B_1$	0	1/8	1/4	5/8	0	0	0	0	1/4	1/2
$B_9A_5C_2$	5/16	9/16	1/8	0	5/8	0	0	1/4	0	0
$B_9H_5A_2$	1/8	9/16	0	5/16	1/4	0	0	0	5/8	0
$B_9H_5C_2$	0	9/16	1/8	5/16	0	0	0	1/4	5/8	0
$H_2A_1B_1$	1/4	1/4	0	1/2	0	0	1/2	0	1/2	0
$C_4H_2A_1B_1$	1/8	1/8	1/2	1/4	0	1/4	0	1/4	0	1/2
$B_9C_4H_2A_1$	1/16	9/16	1/4	1/8	1/8	0	0	1/2	1/4	0

error is as large or larger than the contrast, the contrast is nonsignificant. If the contrast is larger than two times the standard error, the contrast is significant at approximately the .05 level.

In order to make valid interpretations, Model 8 assumes that there is no dominance effect within breed, no grandmaternal effect, no parental heterosis, no sex-linked effect and no epistatic effect. Also, Elzo et al. (1990) mentioned that this kind of procedure must assume that sire and dam direct additive genetic effects are equal.

Results and Discussion

The estimates of direct and maternal additive genetic effects and direct and maternal heterosis effects for BWT, WWT and ADG are presented in Table 25. Direct and maternal additive genetic effects of A, B and C are expressed as a deviation from the Hereford direct and maternal additive genetic effects. Contrasts among genetic effects are shown in Table 26.

Birth weight Angus, B and C direct additive genetic effects for BWT were significantly different from H ($P<.05$). The direct additive genetic effects of Brahman (g_B^I) and Charolais (g_C^I) were greater than that of Hereford (g_H^I), while the Angus direct additive genetic effect (g_A^I) was smaller than H. BWT direct additive genetic estimates were -2.85±1.00, 4.25±1.03 and 7.21±1.02 kg for A, B, and C, respectively. Many published papers have found the Angus direct additive genetic

Table 25. Genetic effects and standard errors for birth weight($\beta_1 \pm se$), weaning weight($\beta_2 \pm se$) and preweaning average daily gain($\beta_3 \pm se$)

Genetic effect[a]	$\beta_1 \pm se$(kg)	$\beta_2 \pm se$(kg)	$\beta_3 \pm se$(kg)
g_A^I	-2.85±1.00*	-10.52±5.56	-.0372±.0254
g_B^I	4.25±1.03*	-6.74±5.69	-.0536±.0260*
g_C^I	7.21±1.02*	19.98±5.82*	.0624±.0267*
h_{AB}^I	3.71±0.75*	37.32±3.62*	.1651±.0163*
h_{AC}^I	-1.02±1.29	11.97±6.17	.0640±.0274*
h_{AH}^I	2.17±1.16	16.48±5.43*	.0699±.0239*
h_{BC}^I	2.75±0.77*	31.00±3.73*	.1382±.0168*
h_{BH}^I	3.52±0.86*	34.49±4.10*	.1514±.0183*
h_{CH}^I	0.85±1.30	11.86±6.19	.0539±.0275
g_A^M	1.08±0.89	20.49±4.71*	.0946±.0215*
g_B^M	-6.89±0.92*	25.52±4.84*	.1583±.0220*
g_C^M	0.31±0.92	28.52±4.97*	.1404±.0228*
h_{AB}^M	0.11±0.78	2.97±3.70	.0138±.0165
h_{AC}^M	1.40±1.34	3.83±6.56	.0104±.0294
h_{AH}^M	2.49±1.28	17.07±6.19*	.0725±.0275*
h_{BC}^M	-0.93±0.78	3.15±3.72	.0197±.0165
h_{BH}^M	1.03±0.78	16.81±3.67*	.0775±.0164*
h_{CH}^M	3.66±1.23*	18.13±6.05*	.0719±.0271*

[a]See text for abbreviations
*P<.05

Table 26. Contrast among genetic effects and their respective standard errors for BWT ($\beta_1 \pm se$), WWT ($\beta_2 \pm se$) and ADG ($\beta_3 \pm se$)

Contrast	$\beta_1 \pm se$(kg)	$\beta_2 \pm se$(kg)	$\beta_3 \pm se$(kg)
Direct additive			
A,C,H vs B	-2.80±0.86*	9.89±4.74*	.0621±.0217*
A,H vs C	-8.64±0.90*	-25.23±5.13*	-.0810±.0236*
Maternal additive			
A,C,H vs B	7.15±0.79*	-9.18±4.08*	-.0799±.0185*
A,H vs C	0.85±0.81	-18.27±4.36*	-.0931±.0200*
Direct heterotic			
AB vs BH	0.19±0.80	2.83±3.78	.0137±.0167
AC vs CH	-1.87±1.55	0.11±7.48	.0101±.0333
B vs other	2.66±0.98*	20.83±4.67*	.0890±.0208*
AB,BH vs BC	0.87±0.62	4.91±3.04	.0201±.0136
AC,CH vs AH	-2.26±1.19	-4.57±5.58	-.0109±.0246
Maternal heterotic			
AB vs BH	-0.92±0.66	-13.84±3.12*	-.0637±.0139*
AC vs CH	-2.26±1.76	-14.30±8.33	-.0615±.0369
B vs other	-2.45±0.97*	-5.37±4.85	-.0146±.0218
AB,BH vs BC	1.50±0.65*	6.74±3.11*	.0259±.0138
AC,CH vs AH	0.04±1.27	-6.09±6.09	-.0313±.0270

A=Angus; B=Brahman; C=Charolais; H=Hereford
*P<.05

effect to be less than that of the Hereford breed (Alenda et al., 1980; Dillard et al., 1980; Neville et al., 1984a; Koch et al., 1985; Cunningham and Magee, 1988; Morris et al., 1994). The estimates reported in these papers ranged from -1.0 to -9.5 kg. Wyatt and Franke (1986) found that the Hereford direct additive effect was superior to the Angus breed effect by 2.60 kg.

Charolais had the largest direct additive effect on BWT (7.21 kg) among the four breeds. This result is in agreement with those reported by Alenda et al. (1980), Dillard et al. (1980), Wyatt and Franke (1986) and Olson et al. (1993). However, Cunningham and Magee (1988) found that the Charolais direct additive genetic effect was not different from that of the Hereford breed. The Brahman direct additive genetic effect was greater than Hereford (4.25 kg), which is similar to the result found by Roberson et al. (1986) and Wyatt and Franke (1986). The latter authors found an estimate of 4.80 kg, while Roberson et al. (1986) reported an estimate of 4.60 kg.

Contrasts among direct additive genetic effects (Table 26) showed that there was a significant difference ($P<.05$) between the Brahman direct additive genetic effect and the average of the other three breeds; Brahman was larger by 2.80 kg. There was also a large difference between the average direct additive genetic effects of the British breeds and that of the Charolais breed. The Charolais direct additive

genetic effect was 8.64 kg larger (P<.05) than the average of g_A^I and g_H^I.

Angus and Charolais maternal additive genetic effects were greater than but not significantly different from the Hereford maternal additive genetic effect. Alenda et al. (1980), Koch et al. (1985), Wyatt and Franke (1986) and Morris et al. (1994) found that Angus and Hereford did not differ in maternal additive genetic effects. On the contrary, Dillard et al. (1980) and Cunningham and Magee (1988) reported that the Angus maternal additive genetic effect was larger than that of the Hereford breed whereas Neville et al. (1984a) concluded that the maternal additive genetic effect of Angus was less than that of the Hereford breed.

Contrary to the large direct additive genetic effect, Charolais had a similar maternal additive genetic effect to H for BWT. The estimate in this study was .31±.92 kg. Larger estimates for g_C^M than for Hereford have been reported by Dillard et al. (1980) and Cunningham and Magee (1988). Alenda et al. (1980) and Wyatt and Franke (1986) found smaller estimates for g_C^M than for H. Wyatt and Franke (1986) found a 2.70 kg advantage for Hereford over Charolais, whereas Alenda et al. (1980) found no difference. On average, the Charolais maternal additive genetic effect does appear to not differ from the British breeds (Angus and Hereford).

Brahman, which had a greater direct additive genetic effect than H, had a much smaller maternal additive genetic effect for BWT than Hereford (-6.89±.92 kg). This result reinforces the documentation of the ability of the Brahman cow to restrict calf birth weight (McElhenney et al., 1986; Sacco et al., 1989). This value is close to the estimates of g_B^M reported by Roberson et al. (1986) and Wyatt and Franke (1986). *Bos taurus* breed maternal additive genetic effects were, on average, larger than that of the Brahman by 7.15 kg.

Crosses involving the Brahman breed had positive direct heterosis influences on BWT ($P<.05$), whereas the A-C, A-H and C-H direct heterosis effects were not different from zero. The h_{AC}^I, h_{AH}^I and h_{CH}^I were -1.02±1.29, 2.17±1.16 and .85±1.30 kg, respectively. Alenda et al. (1980), Dillard et al. (1980) and Olson et al. (1993) found that the A-C direct heterosis effect was not different from zero, whereas Wyatt and Franke (1986) found that h_{AC}^I influenced BWT ($P<.01$). The Angus-Hereford direct heterosis effect on BWT was reported significant ($P<.05$) by Koch et al. (1985), Wyatt and Franke (1986) and Morris et al. (1994), whereas Alenda et al. (1980), Dillard et al. (1980) and Neville et al. (1984a) did not find significant influences of h_{AH}^I on BWT. A negative ($P<.01$) C-H direct heterosis effect was noted by Wyatt and Franke (1986) and a positive effect but not different from zero was reported in the papers by Alenda et al. (1980) and Dillard et al. (1980).

Direct heterotic effects for A-B, B-C and B-H were 3.71±.75, 2.75±.77 and 3.52±.86 kg, respectively. Contrasts among direct heterotic effects (Table 26) indicated that the average direct heterotic effect of Brahman crosses was 2.66 kg larger (P<.05) than the average of crosses not involving Brahman. There were no differences among the breed combinations including Brahman. Wyatt and Franke (1986) observed a significant (P<.05) direct heterotic effect for A-B (2.9 kg) and B-H (2.90 kg), but not for h^I_{BC}. Roberson et al. (1986) reported an estimate of 2.20 kg (P<.05) for h^I_{BH}, whereas Olson et al. (1993) found 3.40 kg (P<.01) for h^I_{AB}.

Maternal heterotic influences on BWT were not important, except for that of Charolais-Hereford dams. The h^M_{CH} partial regression coefficient was 3.66±1.23 kg. Alenda et al. (1980) reported a negative but not significant estimate for h^M_{CH}. Maternal heterotic effects for breed combinations including Brahman were, on average, 2.45 kg lower (P<.05) than the average for the other three breed combinations. The average of A-B and H-B maternal heterosis was 1.50 kg larger (P<.05) than the Brahman-Charolais maternal heterosis. However, h^M_{AB} and h^M_{BH}, and h^M_{AC} and h^M_{CH} did not differ in their influences on BWT.

Koch et al. (1985) and Wyatt and Franke (1986) reported a significant maternal heterosis effect for A-H on BWT (P<.05). However, their estimates had the opposite sign. On the contrary, Alenda et al. (1980) and Morris et al. (1994)

did not find this effect significant. Wyatt and Franke (1986) found that A-B, A-C and B-H maternal heterosis influenced BWT ($P<.01$), while the Angus-Charolais maternal heterosis effect was reported not significant by Alenda et al. (1980) and Olson et al. (1993). Contrary to this study, significant h^M_{BH} (Roberson et al., 1986) and h^M_{AB} (Olson et al., 1993) effects have been reported. However, Dillard et al. (1980) and Cunningham and Magee (1988) found that the average maternal heterosis effect of A-C-H crossbred dams was not significant.

In summary, direct additive genetic effects of the four breeds significantly influenced variation in BWT. Charolais had the greatest positive influence on BWT, compared to the Hereford breed, while g^I_A was smallest. Brahman was the only breed having a significantly maternal additive effect on BWT, compared to the Hereford breed, and it was negative. Direct heterotic effects of Brahman crosses were positive and large, but their maternal heterotic effects on BWT were not important. A-C and A-H heterosis (direct and maternal) did not influence BWT, while the C-H maternal heterotic effect was positive and significant.

Weaning weight The direct additive genetic influence of Charolais for WWT was largest and different from Hereford ($P<.05$), whereas g^I_A and g^I_B were less than but not different from Hereford. The g^I_A, g^I_B, and g^I_C were -10.52±5.56, -6.74±5.9 and 19.98±5.82 kg, respectively. The Brahman direct additive

effect was 9.89 kg less (P<.05) than the average of the A, C and H direct additive genetic effect. The g_C^I effect was 25.23 kg larger (P<.05) than the average of the Angus and Hereford direct additive effect.

Alenda et al. (1980) reported that Charolais had the largest (P<.01) positive direct additive effect for WWT, while the Angus effect was negative (P<.01). The estimates found by Alenda et al. (1980) were 16.7 kg for g_C^I and -4.4 kg for g_A^I. Dillard et al. (1980) found that the Charolais direct additive effect was 20.1 kg larger (P<.01) than the g_H^I effect, while the Angus effect was negative and not different from Hereford. Neville et al. (1984a), Koch et al. (1985) and Morris et al. (1994) reported that the Angus direct additive effect was lower (P<.01) than the Hereford effect (5.5, 5.4 and 3.0 kg, respectively). Cunningham and Magee (1988) found that Angus, Charolais and Hereford did not differ in their direct additive genetic effect on WWT. Wyatt and Franke (1986) showed that g_A^I was lower (P<.01) than that of Charolais and Hereford but not different from Brahman. Olson et al. (1993) showed that Brahman and Charolais direct effects were positive (P<.05) compared to the Angus effect. However, Roberson et al. (1986) found that Brahman direct additive effect on WWT was 12.9 kg less (P<.01) than Hereford.

In contrast to the direct additive genetic effects, all breed comparison with Hereford had a significant maternal additive influence on WWT. Maternal additive genetic effects

for Angus, Brahman and Charolais were positive and larger (P<.05) than Hereford. Weaning weight maternal additive genetic effects were 20.49±4.71, 25.52±4.84 and 28.52±4.97 kg for Angus, Brahman and Charolais, respectively. Contrary to the direct additive genetic effect on WWT, the Brahman maternal additive genetic effect was 9.18 kg larger (P<.05) than the average of the A, C and H maternal additive genetic effects; while the g_C^I effect was 18.27 kg larger (P<.05) than the average of the Angus and Hereford maternal additive effects.

The g_A^M effect was considerably larger than the average of effects reported by Dillard et al. (1980), Neville et al. (1984a), Koch et al. (1985) and Morris et al. (1994) (8.12 kg). The Charolais maternal additive effect was similar to the 28.60 kg found by Dillard et al. (1980). Similarly, the Charolais maternal additive influence on WWT was larger than 10.45 kg found by Cunningham and Magee (1988), while g_A^M was similar to that reported by these authors. Wyatt and Franke (1986) found the Angus, Brahman and Charolais maternal additive effects to be positive compared to the Hereford breed. Similarly, Charolais and Brahman maternal additive influences on WWT were reported to be positive but not significant compared to the Angus breed (Olson et al., 1993).

As was found for BWT, all direct heterosis effects of breed combinations involving the Brahman breed had large (P<.05) and positive influences on WWT. Also, the Angus-

Hereford direct heterosis influenced calf WWT (P<.05). The h^I_{AH} and combinations involving Brahman estimates ranged from 16.48 to 37.32 kg, the largest being for Brahman crosses. The h^I_{AC} and h^I_{CH} were not different from zero. Brahman crossed with A, C and H resulted in direct heterosis estimates 20.83 kg larger (P<.05) than crosses among *Bos taurus* breeds (A, C, and H). The Angus-Brahman direct heterosis effect was not different from h^I_{BH}. Similarly, the h^I_{AB} and h^I_{BH}, on average, were the same as h^I_{BC}.

These results are supported by Wyatt and Franke (1986) who found significant (P<.01) and positive effects of direct heterosis for A-B, B-C, B-H and A-H, ranging from 4.8 to 24.2 kg. The h^I_{AC} and h^I_{CH} were not important. The h^I_{AH} was also found to be positive by Dillard et al. (1980), Neville et al. (1984b), Koch et al. (1985) and Morris et al. (1994). The estimates in those studies ranged from 5.0 to 10.7 kg. Alenda et al. (1980) did not observe an important effect for h^I_{AH}. Olson et al. (1993) reported a significant effect of A-B and B-C direct heterosis, while Roberson et al. (1986) found important the h^I_{BH} effect. The h^I_{AC} effect did not influence WWT in the studies by Alenda et al. (1980), Dillard et al. (1980) and Olson et al. (1993). Charolais-Hereford direct heterosis was found significant by Dillard et al. (1980), but not by Alenda et al. (1980).

Maternal heterotic effects on WWT were significant (P<.05) and positive for breed combinations involving the H

(A-H, B-H and C-H). The estimates were 17.07±6.19, 16.81±3.67 and 18.13±6.05 kg for h^M_{AH}, h^M_{BH} and h^M_{CH}, respectively. The other maternal heterotic effects were not important. The h^M_{BH} was 13.84 kg larger (P<.05) than the Angus-Brahman effect. The average of h^M_{AB} and h^M_{BH} was 6.74 kg larger (P<.05) than B-C maternal heterosis effect.

Koch et al. (1985), Wyatt and Franke (1986) and Morris et al. (1994) reported significant effects of h^M_{AH} on WWT (P<.01), while Alenda et al. (1980) did not find this heterosis important. According to Roberson et al. (1986) and Wyatt and Franke (1986), Brahman-Hereford maternal heterosis influenced WWT (P<.01). The Charolais-Hereford maternal heterosis effect on WWT was reported significant by Alenda et al. (1980).

Some researchers found different results for the influence of h^M_{AB}, h^M_{BC} and h^M_{AC} on WWT. Wyatt and Franke (1986) estimated h^M_{AB} at 13.0 kg. Olson et al. (1993) found estimates of 21.4, 7.4 and 22.1 kg for h^M_{AB}, h^M_{AC}, and h^M_{BC}, while Alenda et al. (1980) estimated h^M_{AC} as 13.2 kg. However, Wyatt and Franke (1986) reported no significant influence for h^M_{AC} on WWT.

In summary, the Charolais additive effect had a positive influence on WWT, with both the g^I_C and g^M_C being the largest. Brahman and Angus direct additive effects were also significant and positive. Crossbred calves which included Brahman had the largest and positive influences on WWT, while

crossbred cows which included Hereford were the only dams having significant influences on WWT.

Preweaning average daily gain Partial multiple regression coefficients for genetic effects are shown in Table 25. Brahman and Charolais direct additive effects were different ($P<.05$) from the Hereford breed. The direct additive effect of Charolais was positive, while that of Brahman was negative. The Angus direct additive influence on ADG was not different from the Hereford breed. The g_A^I, g_B^I and g_C^I were -.0372±.0254, -.0536±.0260 and .0624±.0267 kg/d, respectively. The Brahman direct additive effect was .0621 kg/d lower ($P<.05$) than the average direct additive effect of Angus, Charolais and Hereford, while the g_C^I effect on ADG differed ($P<.05$) from the average direct additive effect of the British breeds.

Dillard et al. (1980), Wyatt and Franke (1986) and Morris et al. (1994) did not find differences between the direct additive effects of Angus and Hereford. Cunningham and Magee (1988) found the Angus direct additive effect to be positive relative to the Hereford breed (.10 kg/d; $P<.01$), whereas it was negative ($P<.01$) in the paper by Neville et al. (1984a) and Koch et al. (1985). Charolais had a positive direct additive influence on ADG. This estimate was very close to the estimate reported by Dillard et al. (1980) and smaller than .13 kg/d published by Wyatt and Franke (1986). Cunningham and Magee did not find a difference between g_C^I and

g^{I}_{H}. The Brahman direct additive genetic effect was lower (P<.05) than that of Hereford. Similar results were reported by Roberson et al. (1986) and Wyatt and Franke (1986).

Angus, Brahman and Charolais maternal additive influences on ADG were significant (P<.05) compared to the Hereford maternal effect. The Brahman, Charolais and Angus maternal additive effects on ADG were .1583, .1404 and .0946 kg/d greater than Hereford. Based on contrasts in Table 26, the maternal additive effect of Brahman was significantly larger (.0621 kg/d, P<.05) than the average maternal additive effects of *Bos taurus* breeds. British breed maternal additive effects were .0810 kg/d lower (P<.05) than the maternal additive effect of Charolais.

Many authors found a positive maternal additive effect of Angus compared to Hereford (Dillard et al., 1980; Neville et al., 1984a; Koch et al., 1985; Wyatt and Franke, 1986; Cunningham and Magee, 1988; Morris et al., 1994). The estimates in those studies ranged from .01 kg/d to .19 kg/d. As in the present study, a Brahman maternal additive effect was also reported to be positive by Roberson et al. (1986) and Wyatt and Franke (1986). The g^{M}_{C} in this study (.1404 kg/d) was very similar to the .13 kg/d reported by Dillard et al. (1980). On ther hand, Cunningham and Magee (1988) did not find differences between Charolais and Hereford maternal additive genetic effects.

All direct heterosis effects had positive and significant (P<.05) influences on ADG, except the Charolais-Hereford effect. As was found for BWT and WWT, breed combinations involving Brahman had the largest direct heterotic influences on ADG. The direct heterosis estimates ranged from .0539 (for h^I_{CH}) to .1651 kg/d (for h^I_{AB}). Similarly, the average of h^I_{AB}, h^I_{BC} and h^I_{BH} was .0890 kg/d larger (P<.05) than the average of h^I_{AC}, h^I_{AH} and h^I_{CH}. On average, there was no differences between h^I_{AC} and h^I_{CH} and h^I_{AH}, or between h^I_{AB} and h^I_{BH} and h^I_{BC}. In the same way, the Angus-Brahman direct heterotic effect was the same as the Brahman-Hereford effect.

The direct effect of A-B heterozygosity increased ADG by .1651 kg/d (P<.05). Wyatt and Franke (1986) observed a lower value, .10 kg/d, for its effect on ADG. Brahman-Hereford direct heterosis also increased ADG (.1514 kg/d, P<.05). This estimate was lower than those reported by Roberson et al. (1986) and Wyatt and Franke (1986). The latter authors also found a lower value for the Brahman-Charolais direct heterosis effect, .0980 kg/d. Contrary to the .0640 kg/d (P<.05) for h^I_{AC}, Dillard et al. (1980) and Wyatt and Franke (1986) reported no effect of A-C heterozygosity on ADG. Lower values for Angus-Hereford direct heterotic effects on ADG have been reported (Dillard et al., 1980; Koch et al., 1985; Wyatt and Franke, 1986; Morris et al., 1994). These authors reported estimates between .0190 and .0310 kg/d.

However, it was similar to the value reported by Neville et al. (1984). The C-H direct heterotic effect found to be nonsignificant in this study, was found significant (P<.05) by Dillard et al. (1980) but not by Wyatt and Franke (1986).

As was found for WWT, maternal heterosis of crossbred dams which included Hereford produced large (P<.05) effects on ADG. All three crosses resulted in increased ADG (P<.05). Wyatt and Franke (1986) observed a similar value for the maternal heterotic effect of Brahman-Hereford on ADG, .0810 kg/d, and a somewhat lower value, .0220 kg/d, for the Angus-Hereford effect. The h^{M}_{AH} was found also lower by Morris et al. (1994), .0490 kg/d. In disagreement with the results in this study, h^{M}_{AB} and h^{M}_{AC} were reported significant by Wyatt and Franke (1986).

In summary, Charolais direct and maternal additive genetic effects were large and significant. All crosses involving the H resulted in increased ADG, except for the C-H maternal heterosis effect. Brahman and Angus had a negative direct additive effect and a positive maternal additive influence on ADG. Crossbred calves involving Brahman were gained quicker, but crossbred dams which included the B did not improve ADG. Angus combined with any other breed resulted in a significant direct heterosis, but it did not help to increase ADG through maternal heterosis.

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CONCLUSIONS

Based on the results obtained from this study, the following conclusions can be made:

- The maternal permanent environmental effects were not important in explaining variation of preweaning growth traits. The extent to which these insignificant effects could be the result of sampling error or the result of some unknown source of bias was not clear.
- The maternal additive genetic variance appeared to be extremely important in explaining the phenotypic variation of preweaning growth traits. Ignoring this effect overestimated σ_A^2 and h_A^2. The maternal additive genetic variance was more important for WWT and ADG than for BWT.
- Fitting direct-maternal additive genetic covariance significantly contributed to a better fit of the data. Estimates of the genetic correlation between direct and maternal additive effects were positive for BWT and negative for WWT and ADG.
- Preweaning growth traits were determined more by genetic characteristics of the calf than those of the dam. Direct heritability estimates were moderate to high, while estimates of maternal heritabilities were low to moderate.
- There should be little loss in genetic progress for the maternal traits when selection is applied to direct and maternal effects as total heritability was close to the direct heritability. The magnitude of heritability estimates

indicates that opportunity exists to improve these traits through selection

- The direct additive genetic correlations among pre-weaning growth traits were positive. The largest genetic correlation was between WWT and ADG.
- The maternal additive genetic correlations among pre-weaning growth traits were positive. Again, the largest genetic correlation was between WWT and ADG.
- All direct-maternal additive genetic correlations among preweaning growth traits were positive, except for WWT-ADG.
- Charolais had the largest direct additive genetic influence on preweaning growth traits and had the largest maternal additive genetic influence on WWT, compared to the Hereford breed.
- The Brahman had positive direct additive genetic influences for BWT and had negative direct additive influences for ADG, compared to the Hereford breed.
- Angus had negative direct additive genetic effects and had positive maternal additive genetic effects on preweaning growth traits, compared to the Hereford.
- Brahman was the only breed having a significantly maternal additive effect on BWT. All breeds exhibited positive maternal additive influences on WWT and ADG.
- All direct heterotic effects were positive, except for Angus-Charolais for BWT. Crossbred calves involving the Brahman were the most positive.

- Birth weight was not influenced by maternal heterosis, except for Charolais-Hereford maternal heterotic effect. Maternal heterotic effects involving the Hereford were the only positive and significant effects on WWT and ADG.
- For WWT and ADG, both direct and maternal genetic effects need to be taken into account to optimize selection response. Selection solely for direct genetic effects does not lead to improvement of the cow's maternal ability, and could even result in deterioration of the maternal ability.

APPENDIX

Table 27. Estimates of phenotypic variances for BWT, WWT and ADG when fitting six different models

Model/Trait	BWT	WWT	ADG
1	27.62	579.16	.01143
2	27.61	579.10	.01143
3	27.40	591.97	.01177
4	27.31	593.31	.01181
5	27.39	591.84	.01177
6	27.30	592.83	.01180

Table 28. Empirical correlations among variance components under Model 4

Trait	BWT		WWT		ADG	
Component	σ^2_M	σ_{AM}	σ^2_M	σ_{AM}	σ^2_M	σ_{AM}
σ^2_A	.94	-.45	.40	-.74	.47	-.77
σ^2_M		-.38		-.74		-.79

VITA

Denis José Salgado Fonseca, son of Miriam Salgado and José Fonseca, is a native of Chontales, Nicaragua. He attended public schools in Chontales and graduated from High School of Santo Tomás, Chontales in December 1978. In February, 1979 he entered University of Nicaragua where he received a Bachelor of Science degree in Animal Science, graduating in December 1984. In September, 1986 he entered Graduate School at Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), an international agricultural center based in Costa Rica, where he was awarded a Master of Science degree in Tropical Animal Production in October 1988. He joined the Department of Animal Science at Louisiana State University in January, 1992 to pursue a Doctor of Philosophy in Animal Breeding and Genetics.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Denis Jose Salgado-Fonseca

Major Field: Animal Science

Title of Dissertation: Estimation of Genetic Parameters For Preweaning Growth Traits of Crossbred Cattle

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

February 14, 1995